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SOME TROPHIC RELATIONS IN RUNNING WATERS

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SUMMARY

The ecology and proximate composition of some plants and animals in running waters were studied in an attempt to elucidate some aspects of the relationships between different trophic levels. Although algal communities almost always showed a spring bloom, apparently in response to increasing day length, the standing crop subsequently showed considerable variation. This was often attributable to such factors as either the direct or indirect effects of flooding or to the interactions between communities. No marked seasonal trends were observed in the amount of lipid found in algae from field collections, contrasting with the situation in the larval lamprey, a microherbivore. Algae generally made only a small contribution to the total organic fraction of the suspended and epilithic material. Although the microflora formed an important component of the diet of *Asellus* and *Gammarus*, only in the case of *Paramecium* were microphagus feeders apparently effecting the standing crop. Lampreys accumulated large neutral lipid reserves at the end of both the larval microphagous and adult carnivorous stages, an adaptation to the metabolic demands of the subsequent lengthy non-trophic phases. The vertical distribution, degree of motility and seasonal changes in the biology of various crustacean species were important in determining their use as a teleost food source. Other factors affecting fish feeding were hunting behaviour, visual acuity, mouth morphology and dimensions, and the temperature and turbidity of the water.

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1. General Introduction

The formation of plant material through the photosynthesis and division of algae i.e. primary production, is a major source of energy in large bodies of water. There is a growing realization, however, that decaying plant matter originating from terrestrial sources, namely allochthonous material, plays a key role in the energy cycle of rivers and small lakes (e.g. Efford, 1969). Algae, decaying organic material of aquatic origin and allochthonous substances are used by herbivores in the water for the formation of mainly lipid and protein. This process, termed secondary production, subsequently provides food for first rank carnivores (tertiary production) which in turn supports quaternary production by second rank carnivores. These stages of production are known as trophic levels and between each level there is usually a considerable decrease in the total amount of organic material. These losses take place mainly because most of the assimilated food provides energy for resting and active metabolism rather than for growth (e.g. Elliott, 1973) and because at least some of the food ingested by animals is not absorbed (e.g. Prus, 1971).

The rate of primary production is significantly effected by the concentration of inorganic and organic substances in the environment, the intensity and duration of solar radiation and the temperature of the water. Since for much of the year the level of the last two parameters is, in the northern temperate zone, generally unsuitable for rapid production (Lund, 1970), the density of the microflora in this region remains low in both rivers and lakes. During the summer, on the other hand, inorganic nutrients frequently limit growth, particularly in lakes where these substances are lost to the hypolimnion during thermal stratification (Lund, 1971). Although nitrogen, phosphorus, silicon and carbon are important in regulating growth (Lund, 1970, 1971; Dickman, 1973), the concentration of many other nutrients, such as iron, manganese, molybdenum and cobalt, as well as several different vitamins, may exert significant control over the flora (Lund, 1964; Lange, 1974; Swift and Taylor, 1974). As pointed out by Round(1971), there has been considerable progress in obtaining an accurate correlation between environmental conditions and the standing crop of planktonic algae in lakes, but data concerning the algae in floating waters are almost completely lacking. Furthermore, since the limited work in these latter areas has invariably centered on only one particular community, an overall picture of the interactions of the different assemblages has yet to be described. Finally, although several estimates of the standing crop are available for different assemblages (Moss and Round, 1967; Hickman, 1971), an accurate assessment of their abundance relative to decaying organic material has not been made.

The chief organic products of primary production fall into three main categories: protein, lipid and carbohydrate. Variation in the quantity and digestibility of these substances in both algae and dead plant material play a key role in determining the rate of secondary production. Barlocher and Kendrick (1973), for example, found a 100% difference in the growth rate of the amphipod Gammarus pseudolimnaeus Bousfield when it was fed on leaves or fungi representing different species. Although much data are available concerning the nutritive value of allochthonous material (Kaushik and Hynes, 1968, 1971) and of artificially cultured algae (e.g. Harris and Riley, 1956; Demort et al., 1972), information is lacking on the chemical composition of algal species taken directly from the field.

There have been numerous investigations on the feeding biology of herbivores but, in most instances, a comprehensive picture is not available for any one species. For example, in the case of the isopod Asellus aquaticus L. and the amphipod Gammarus pulex L., both of which are abundant in streams throughout Europe (Hynes, Macan and Williams, 1960) previous work has emphasized the importance of decaying organic matter (e.g. Haempel, 1908; Minshall, 1967) and has largely ignored the algal component of the diet. On the other hand, in larval lampreys, a group of animals which in many rivers are the predominant vertebrate (Hardsity and Potter, 1971a), the studies have concentrated mainly on algae (e.g. Creaser and Hann, 1929; Moore and Beamish, 1973). Since, as outlined earlier, the type of food consumed by herbivores may greatly effect the rate of secondary production, it is important that our current knowledge on the feeding biology of these animals is expanded. Apart from food, numerous aspects of a species life history, such as reproductive biology, movements and gross morphological changes, may also significantly influence the level of organic material. In the case of lampreys for example, a considerable decline in wet weight, coupled with a depletion of energy reserves, occurs during metamorphosis and the spawning migration (Hardisty and Potter, 1971b; Lowe, Beamish and Potter, 1973).

A complete understanding of the factors which affect the rate of tertiary and quaternary production in natural populations of carnivores depends on a reasonably comprehensive knowledge of the feeding biology of these animals, as was also the case with herbivores. To date, much of the literature dealing with the consumption of prey has emphasized the quantities and type of food consumed rather than the basis of food selection.

This study has investigated aspects of the interrelationships between the various trophic levels in running waters and some of the factors influencing the rate of production. In the case of algae, special emphasis has been placed on the standing crops of both true planktonic and detached forms (potamoplankton) and on those living on the sediment (epipelic) and attached to rocks(epilithic), sand grains (episammic) and macrophytes (epiphytic). Proximate and fatty acid analyses were employed to ascertain whether seasonal changes in abundance and environmental conditions were accompanied by parallel changes in the chemical composition of the algae. Consideration was then given to the role which both the microflora and decaying material played in the environment and in the diet of certain herbivores. For one of these animals the rate of lipid deposition was then considered from the point of view of changes with season and age and an attempt made to relate these to algal and detritus variation and to particular aspects of the animal's life cycle. Finally, first rank carnivorous fish were considered in terms of their feeding behaviour and morphology and the abundance of prey. In one second rank carnivore, the amount of lipid was measured at the end of the trophic phase and its subsequent decline followed through the animal's migration to the spawning grounds.

2. The Seasonal Succession of Algae in Streams and Rivers

Introduction

Although algae frequently contribute greatly to the energy cycle of streams and rivers (Hynes, 1970), relatively little is known about the factors which control the species composition and standing crop of the different communities (Brown, 1908; Round, 1972; Whitton, 1974). In contrast, a great deal has been written about planktonic algae in still waters (see Round, 1971 and articles listed in the General Introduction). The primary purpose of this study was therefore to describe seasonal changes in the flora of six rivers and to attempt to correlate these with fluctuations in environmental parameters.

Materials and Methods

Epipelic algae were normally sampled at least every two weeks from three sites on each of the six study rivers. The uppermost 2 cm of sediment was collected with an aspirator from an area measuring 30 cm^2 within each site and then transported immediately to the laboratory where the relative abundance of the flora in each sample was usually estimated from a count of 300 (Moore, 1974a,b). Although the number of individual cells of filamentous diatoms was recorded, in the case of chlorophytes and cyanophytes, entire filaments and colonies were counted. The total number of cells in each sample was determined by diluting the material in distilled water to a volume of 100 ml and shaking vigorously for 30 sec. Three 0.01 ml aliquots were taken immediately and all the cells in each aliquot counted, this then enabling an estimate to be made of algal densities on the sediment.

Triplicate samples of planktonic algae were collected in 4 l plastic containers held near mid-stream 0.5 - 0.7 m below the surface of the water. In the laboratory, each sample was shaken vigorously for 30 sec and one aliquot of 0.5 - 1.0 l filtered through a Sartorius membrane (pore size 1.2 μm). The subsequent enumeration of the algae was identical to that outlined above.

Samples of algae attached to *Cladophora glomerata* were collected and analyzed as outlined in Moore (1974c). This involved an initial examination of the flora in a wet mount as outlined above to determine the relative abundance of the different species, a total count of 3,000 usually being made. The sample of *Cladophora* was then dried by sublimation to constant weight and oxidized in a known volume of nitric acid. The number of cells in three 0.01 ml aliquots was estimated, thus permitting a determination of density in terms of the dry weight of *Cladophora*. The flora associated with water cress, *Nasturtium officinale* R. Br., and pond weed, *Groenlandia densa* (L.) Fourr., was examined directly at a magnification of 1,000 times with the method of species analyses remaining unchanged. The epilithic flora was always collected from four sites by scraping 200 - 300 cm^2 of rock surface with a scapel blade, the methods of enumeration remaining similar to those outlined for the epipelic flora.

Although Jones (1974) found that scraping methods may seriously underestimate algal numbers, the efficiency of such techniques undoubtedly depends on the degree of smoothness of the rock and the standing crop and species composition of the flora. In the present study, careful examination of the rocks collected, all of which had a relatively smooth surface, showed that almost all of the attached material was removed.

The volume of common diatoms was estimated by obtaining camera lucida drawings of about 20 specimens of each species and determining the area with a Hayashi Denko automatic area meter (Type AAM-5). The average depth of the actual cells was then determined at a magnification of 1,000 times, thus enabling an estimate to be made of the volume. In the case of algae other than diatoms, the average cell volume was estimated from direct measurements of length, breadth and depth as outlined in Moore (1974a).

Daily rates of growth and disappearance of algae were determined from changes in standing crop values between two consecutive sampling periods (Stockner and Armstrong, 1971). The silica, orthophosphate, nitrate and total alkalinity content of the water in the plankton samples was determined monthly between June 1973 and June 1974 using heteropoly blue (APHA, 1971), molybdenum blue (Vogel, 1964), phenoldsulfonic acid (Welcher, 1963) and titration (APHA, 1971) procedures respectively. Estimates of the organic content of the upper two cm of sediment were made at monthly intervals by ashing at 550°C for 24 h.

Avon River

The Avon River, which is approximately 120 km in length, flows through mixed farmland. It falls about 115 m from its source to the Severn Estuary and several major population centres are situated on its banks. In the vicinity of the collection sites (Lat. 51° 24' ; Long. 2° 20'), all of which were invariably unshaded and located within 0.5 km of each other, the river was approximately 50 m in width.

Physico-chemical Analyses

Water temperatures (Fig.1) remained relatively constant between February and April when they averaged 9.5°C. They then rose sharply to a plateau of 15°C in June and July before increasing again to reach the vernal peak of 17.5°C in September, after which they fell rapidly to 4.5°C by the end of December. Temperatures subsequently remained low until March of 1974 but then rose quickly reaching 15°C by May. During the remainder of the summer values were comparatively constant (14 - 15°C) but then fell sharply during September and October to the overwintering level of 6 - 7°C.

Several floods occurred during the warmer months of 1973 but by early August the rate of discharge had fallen below 12 m^3 sec^{-1}, a level maintained until the winter (Fig. 2). During the following summer, the rate of water flow remained relatively constant between 5 - 10 m^3 sec^{-1}. Water velocity over the area used for the collection of attached algae generally lay between 2 and 20 cm sec^{-1}, except during flood conditions when values of up to 89 cm sec^{-1} were recorded (Fig. 1). Water depth in these areas usually ranged between 20 and 40 cm, although during flooding they exceeded 1.5 m. The pH of the river water was always relatively high, ranging between 7.5 and 8.2, and although considerable depletion of silica occurred during the late spring and early summer of both years, the other nutrients remained relatively abundant (Table 1). The organic content of the sediments under non-flooding conditions ranged from 8.5 to 21.6% of the total dry weight with an average value of 15.3%.

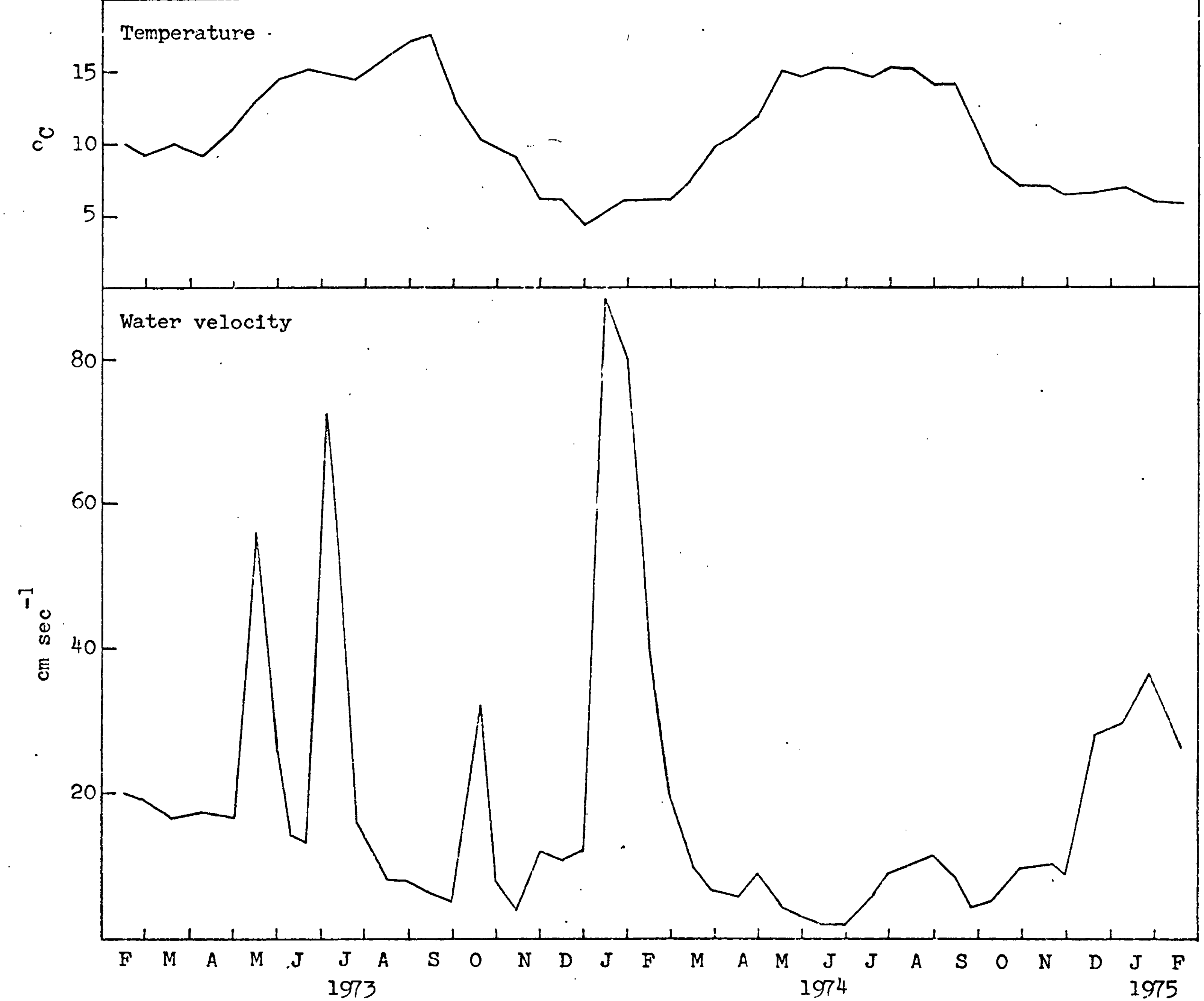

Fig. 1. Seasonal changes in the temperature of the Avon River together with the water velocity over the epipelic collection sites.

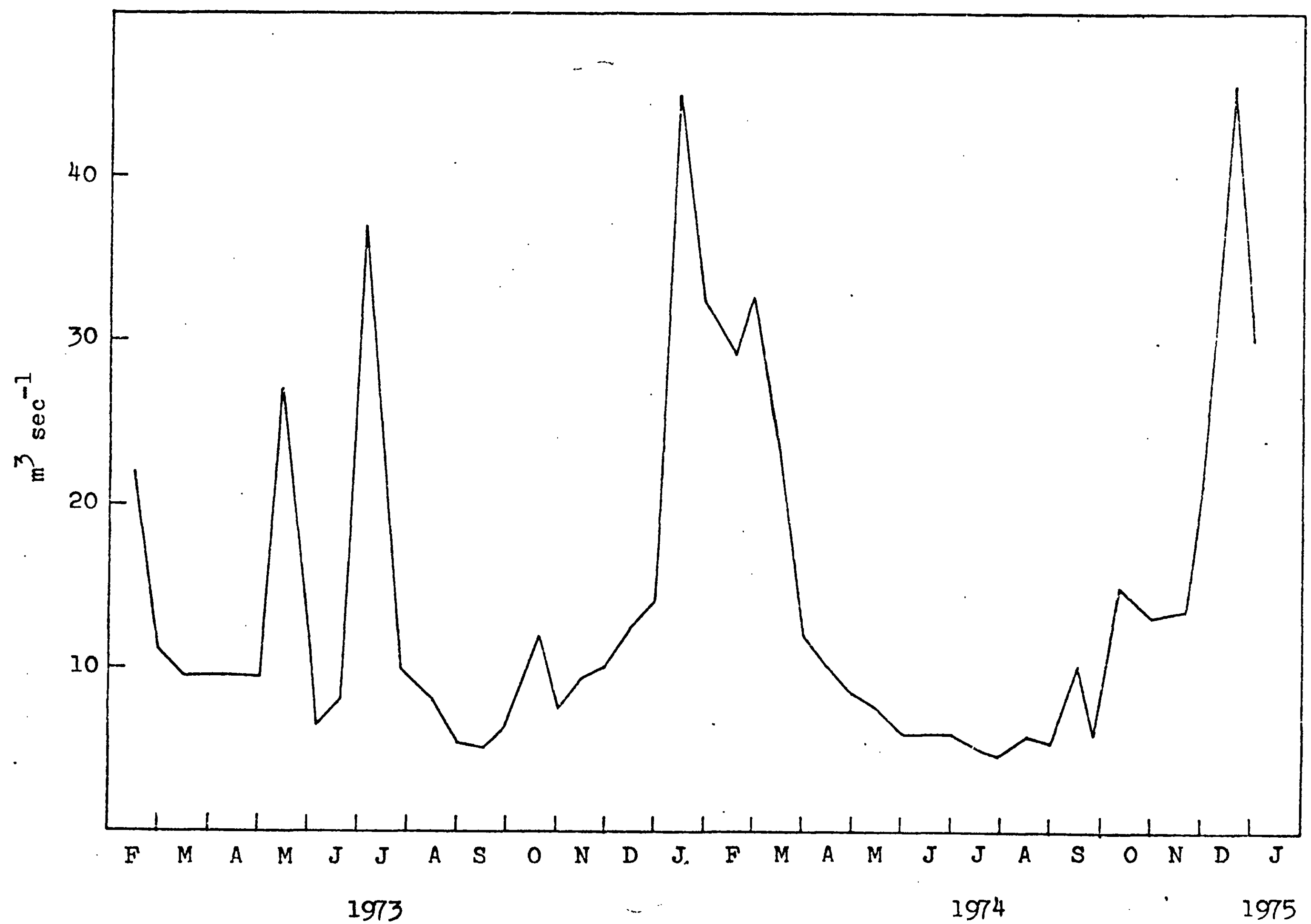

Fig.2 . Seasonal changes in the discharge rate of the Avon River.

Table 1. Physico-chemical properties of water from the Avon River during 1973 and 1974. Except for pH, all data are expressed in terms of mg l^{-1}

Parameter	Average	Range
pH	7.9	7.5 - 8.2
Total Alkalinity	382	275 - 420
Silica	5.4	0.5 - 12.5
Orthophosphate-Phosphorus	0.20	0.05 - 0.4
Nitrate-Nitrogen	5.1	3.4 - 9.5

Epipelic Communities

Two hundred and fifty-two species, varieties and forms of algae were found on the sediments of the Avon River and of these 208 belonged to the Bacillariophyta, 27 to the Chlorophyta, 11 to the Cyanophyta and six to the Euglenophyta. The predominant taxa in the former group of algae included *Nitzschia linearis*, *N. palea* (including variety *debilis* and form *minuta*), *N. acicularis*, *Navicula viridula* v. *minor*, *Surirella ovata* v. *minuta* and *Stephanodiscus hantzschii* (Table 2, Fig. 3). Although *Chlamydomonas monadina* was the only chlorophyte to account for more than 10% of the epipelic flora on one or more occasion (Table 2), *Scenedesmus* spp. (especially *Scenedesmus quadricauda* and *S. obliquus*) were also relatively important (5 - 6%) in some instances. *Oscillatoria limosa* was the only common member of the Cyanophyta, while euglenoids, represented mainly by *Trachelomonas volvocina* and *T. volvocina* v. *minuta*, were invariably rare.

Many of the predominant epipelic diatoms exhibited recurring patterns of seasonal abundance at all three collection areas, but striking differences in the actual numbers of these species occurred during the periods of peak growth in the two different sampling years (Fig. 3). For example, *Nitzschia linearis*, *N. sublinearis* and *N. acicularis*, although normally rare on the sediment, achieved considerable importance during the spring of 1973 (9.25×10^5, 3.9×10^5 and 14.0×10^5 cells cm^{-2} respectively), but maintained relatively small numbers (4.25×10^5, 2.8×10^5 and 1.6×10^5 cells cm^{-2} respectively) during a comparable time in 1974. Although a small difference existed in the timing of the maxima of the first two species, the greatest recorded development of *Nitzschia acicularis* occurred in both years at virtually the same time in April. *Nitzschia palea* occurred in relatively large numbers between February and April 1973, with the maximum standing crop, 5.6×10^5 cells cm^{-2}, being observed in the middle of March. During 1974, however, this species was comparatively low in density and only achieved considerable abundance, i.e. 1.6×10^5 cells cm^{-2}, near the beginning of April. In contrast to the patterns exhibited by *Nitzschia* spp., the highest density, 6.75×10^5 cells cm^{-2}, of *Surirella ovata* v. *minuta* was recorded in 1974. The time of maximum development for each of the two years differed by only five days. During both 1973 and 1974, *Navicula*

Table 2. List of epipelic algae collected from the Avon River which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes minutissima v. *cryptocephala*
Amphora ovalis v. *pediculus*
Cocconeis placentula v. *euglypta*
Cyclotella meneghiniana
Cyclotella stelligera v. *tenuis*
Melosira varians
Navicula gregaria
Navicula salinarum v. *intermedia*
Navicula viridula v. *minor*
Nitzschia acicularis
Nitzschia dissipata
Nitzschia linearis
Nitzschia palea
Nitzschia palea v. *debilis*
Nitzschia sublinearis
Rhoicosphenia curvata
Stephanodiscus hantzschii
Surirella ovata v. *minuta*
Chlamydomonas monadina
Oscillatoria limosa

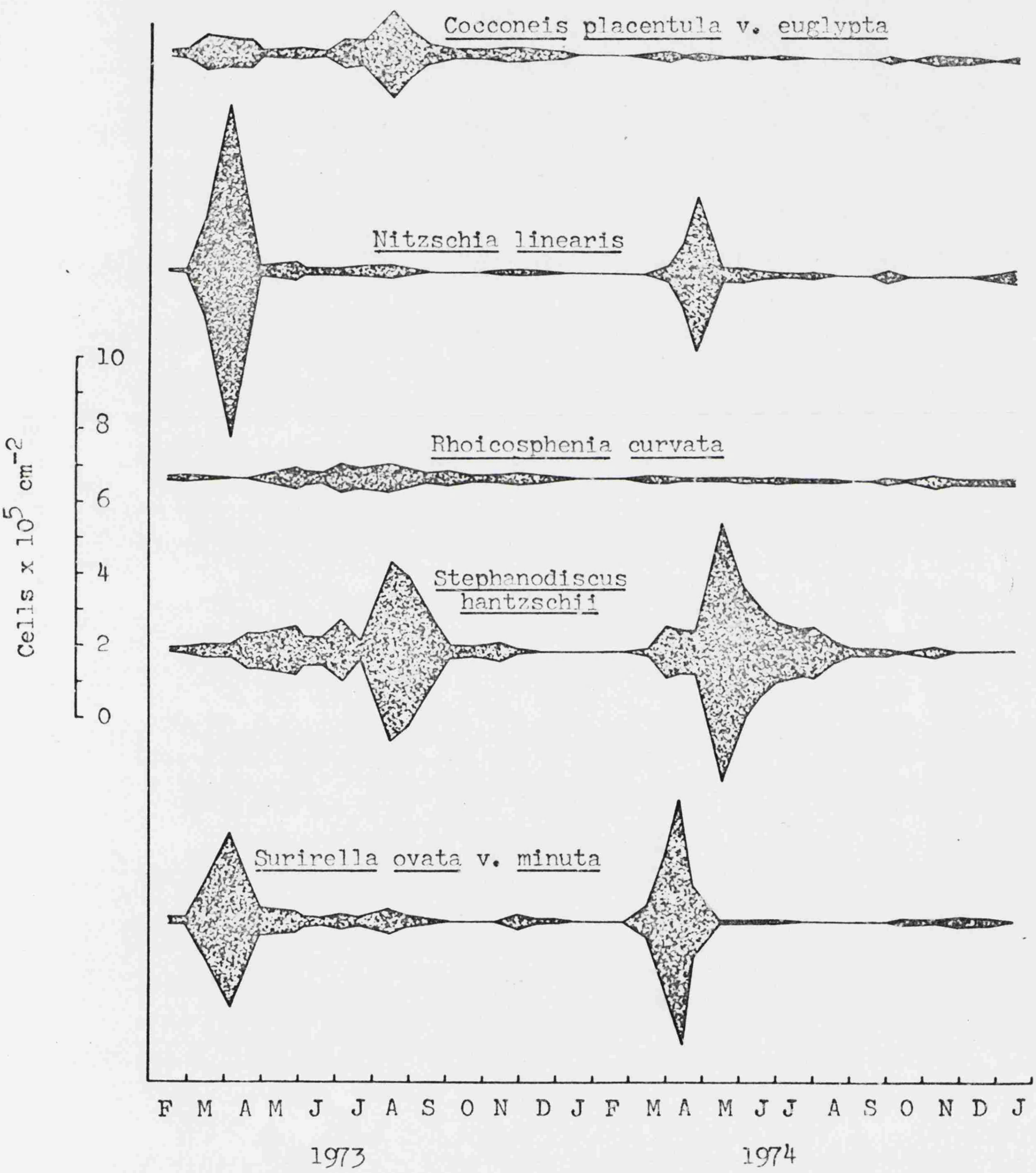

Fig. 3. Seasonal changes in the standing crop of common epipelic algae in the Avon River.

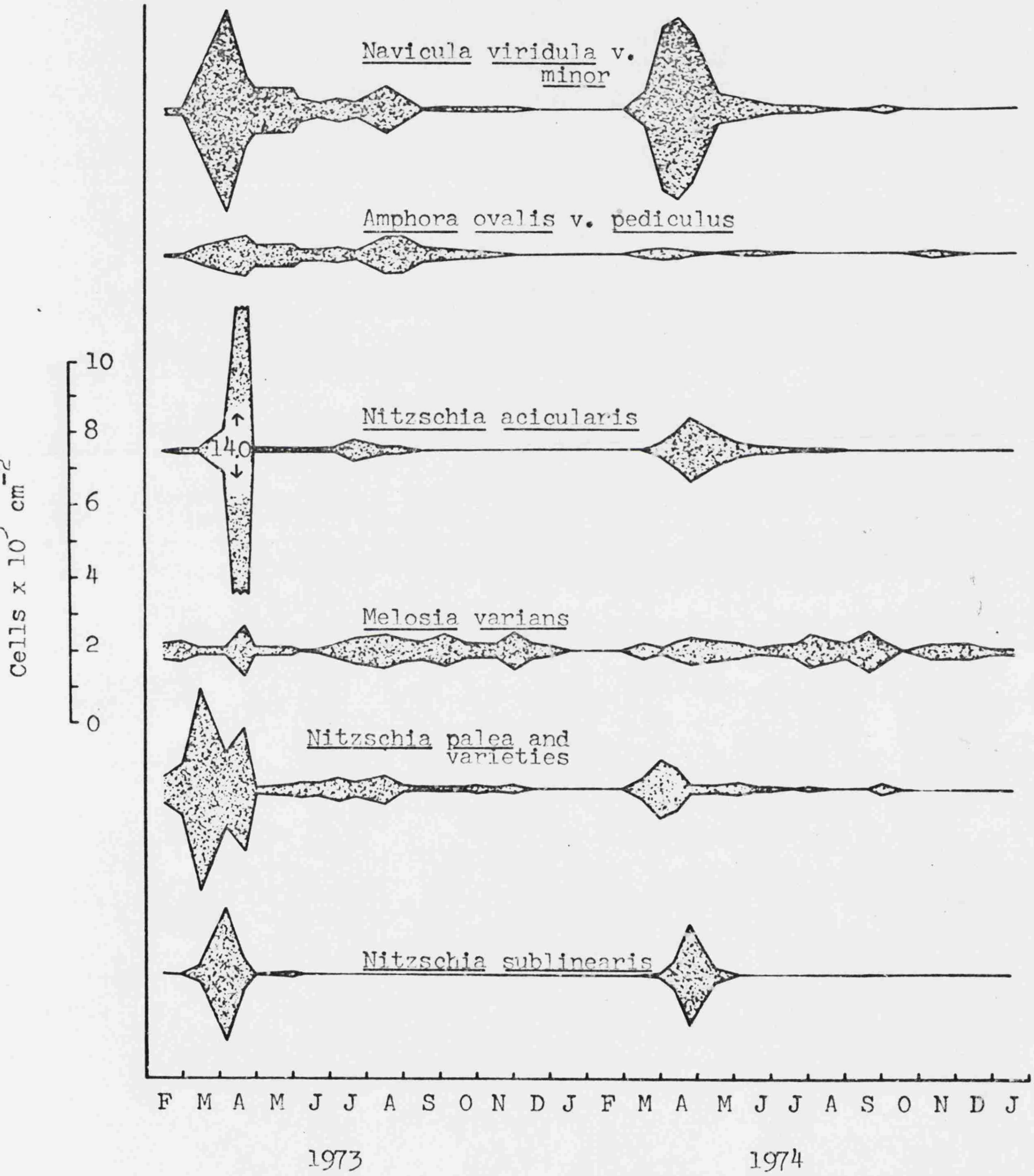

Fig. 3 (Cont'd). Seasonal changes in the standing crop of common epipelic algae in the Avon River.

viridula v. minor reached peak abundance at the same time as S. ovata v. minuta. However, the maximum standing crop, 5.0×10^5 cells cm^{-2}, of the former species in 1974 was smaller than that recorded in 1973, i.e. 5.6×10^5 cells cm^{-2}. Amphora ovalis v. pediculus, Cocconeis placentula v. euglypta and Rhoicosphenia curvata, usually occurred in relatively small numbers, i.e. less than 1.0×10^5 cells cm^{-2}, during the spring, summer and autumn of both years. Distinct blooms were usually not observed, but in the case of C. placentula v. euglypta a sharp rise in abundance from 0.8×10^5 to 2.5×10^5 cells cm^{-2} occurred during August 1973. Stephanodiscus hantzschii, although normally planktonic, maintained a large population on the sediments during the warmer months of both years. During 1973, the greatest density of this species, 5.0×10^5 cells cm^{-2}, occurred in August, whereas in 1974 the highest value, 7.2×10^5 cells cm^{-2}, was recorded in May.

The total standing crop of the epipelic flora increased from relatively low values, 0.3×10^6 cells cm^{-2}, in February to more than 3.0×10^6 cells cm^{-2} during April and May (Fig.4). Thereafter, numbers fell, coincident with the repeated periods of flooding, and did not recover until the middle of August when the density reached 2.2×10^6 cells cm^{-2}. The numbers of algae subsequently fell more or less continuously until March 1974 when a sharp rise to 2.5×10^6 cells cm^{-2} occurred. The abundance of the flora subsequently decreased without interruption until the winter and thereafter levelled off at approximately 1,000 cells cm^{-2}. Seasonal changes in the density of the algae in terms of cell volume roughly paralleled those outlined above. However, the greatest quantity of algae recorded in 1974, 3.5×10^9 $\mu m^3 \cdot cm^{-2}$, exceeded the maximum of 1973, i.e. 3.1×10^9 μm^3 cm^{-2}.

The fastest daily growth rate of the epipelic flora, 10.3×10^4 cells cm^{-2}, occurred during March and April of 1974 while slower rates of 8.0×10^4 and 7.75×10^4 cells cm^{-2} were recorded during August 1973 and March/April 1973 respectively (Fig.4). In terms of cell volume, the fastest daily rates also occurred during the same periods as above, with the maximum value being 10.3×10^7 μm^3 cm^{-2} (Fig.4). Disappearance of the algae from the sediments took place most rapidly during May 1973 when daily rates of loss of

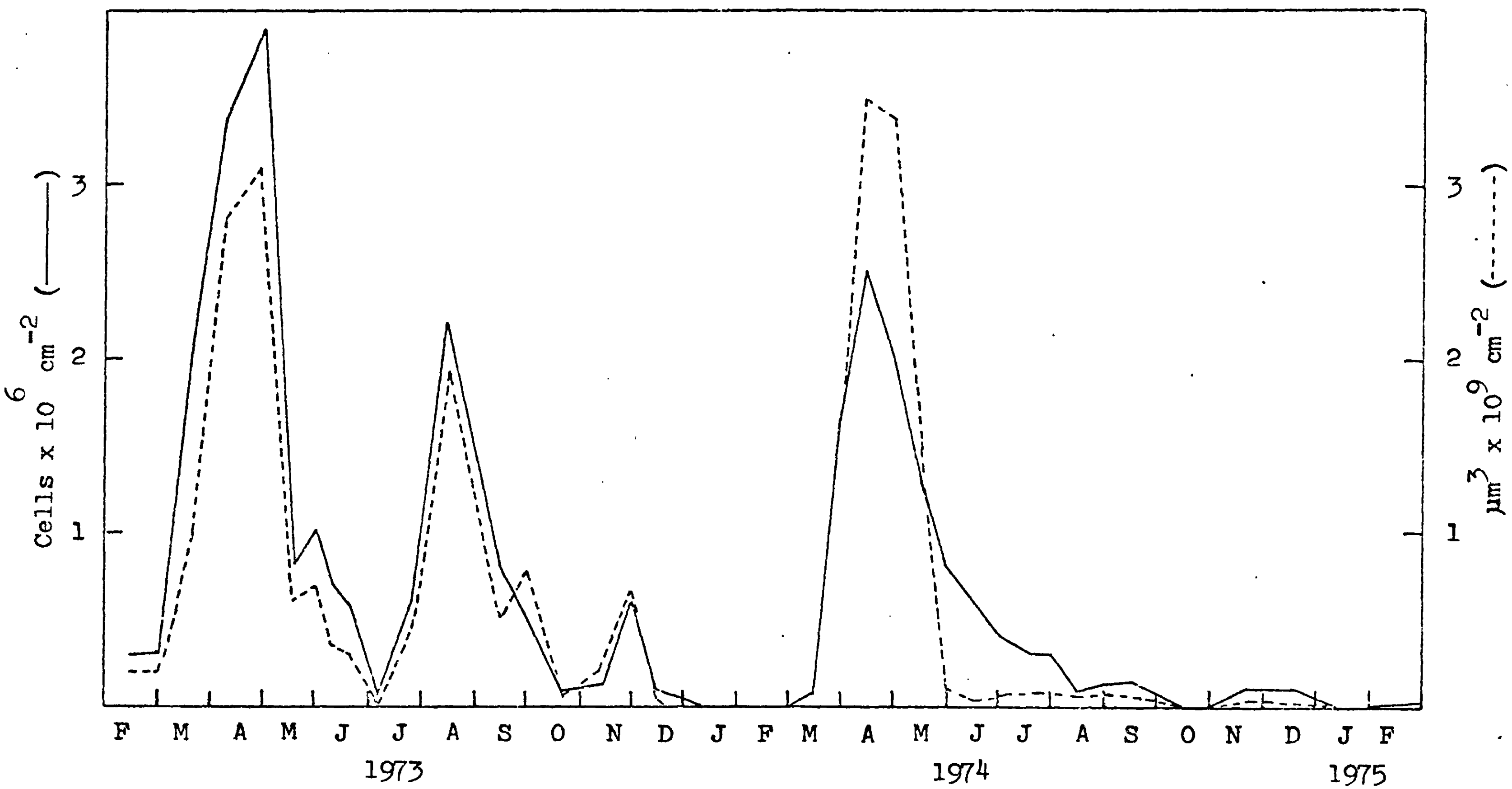

Fig. 4. Seasonal changes in the standing crop of the entire epipelic assemblage in the Avon River.

20.7×10^4 cells cm^{-2} were observed, followed by values of 4.7×10^4 cells cm^{-2} in August and September 1973 and 4.0×10^4 cells cm^{-2} in April and May 1974. The corresponding respective values in terms of cell volume during the above periods were 16.7×10^7, 5.0×10^7 and 11.0×10^7 μm^3 cm^{-2}.

Epilithic Communities

Since most of the rocks in the Avon River were covered with Cladophora glomerata and this limited the growth of the smaller epilithic forms on these substrates, collections of the epilithic assemblage were restricted to small rocks of 5 - 15 cm diameter where the macrophyte was absent.

The epilithic assemblage in the Avon River consisted of 93 different species, varieties and forms of diatoms, while the numbers of chlorophytes, cyanophytes and euglenoids were nine, eight and four respectively. The predominant members of the first group of algae included Melosira varians, Nitzschia dissipata, Navicula viridula v. minor and Diatoma vulgare with Oscillatoria limosa and Lyngbya spp. being the most frequently encountered members of the Cyanophyta (Table 3, Fig. 5). In the case of chlorophytes and euglenoids, which invariably occurred only in small numbers, the most frequent genera were Scenedesmus, Oedogonium and Euglena.

In contrast to the epipelic communities, the number of epilithic algae formed a less clear correspondence between the two sampling years (Fig. 5). For example, Melosira varians showed considerable development during much of 1973, reaching its greatest numbers, 3.5×10^5 cells cm^{-2}, by the middle of August, whereas in 1974 much smaller populations were maintained and the peak abundance, 1.4×10^5 cells cm^{-2}, was observed at the beginning of June. Similarly, the density of Nitzschia dissipata and Rhoicosphenia curvata increased sharply during August and September in 1973 to values far in excess of those ever found in 1974. With respect to abundance, differences were also found in the density of Navicula viridula v. minor but here the greatest values, 5.7×10^5 cells cm^{-2}, were found in 1974 rather than 1973. Although Diatoma vulgare also maintained a larger population in 1974 compared with 1973, the period of peak abundance coincided in both years.

Table 3. List of epilithic algae collected from the Avon River which accounted for more than 10% of the flora on at least one sampling date.

Cocconeis pediculus
Cocconeis placentula v. *euglypta*
Diatoma vulgare
Diatoma vulgare v. *producta*
Melosira varians
Navicula tripunctata
Navicula viridula v. *minor*
Nitzschia dissipata
Nitzschia dissipata v. *media*
Nitzschia palea
Rhoicosphenia curvata
Surirella ovata v. *minuta*

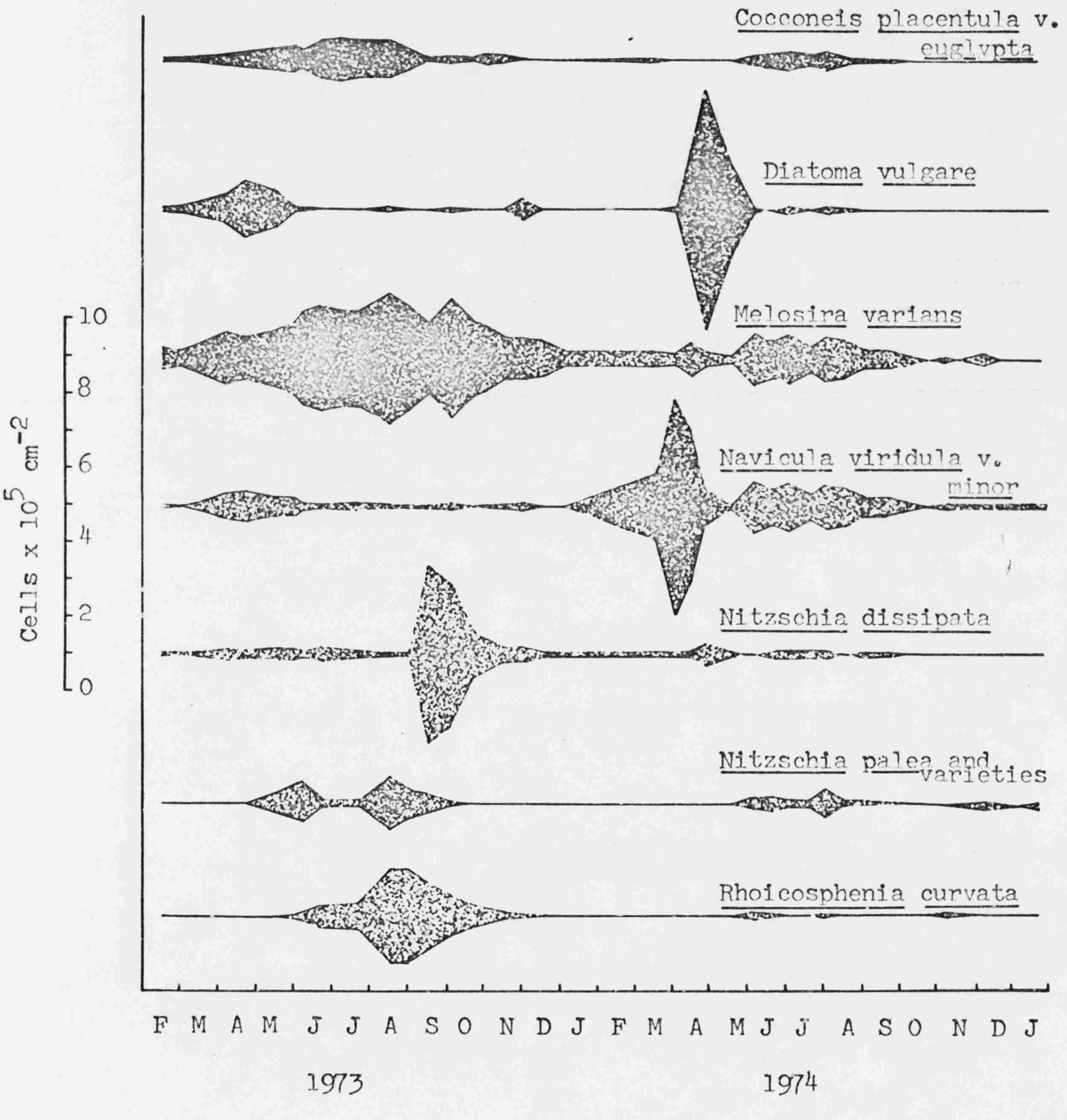

Fig. 5. Seasonal changes in the standing crop of common epilithic algae in the Avon River.

The total standing crop of the epilithic flora increased more or less continuously throughout the first part of the investigation reaching a maximum value of 1.95×10^{6} cells cm^{-2} during September (Fig. 6). Although the numbers then fell sharply, resulting in a density of less than 1,000 cells cm^{-2} in January and February of 1974, a precipitous rise to 0.9×10^{6} cells cm^{-2} occurred during the following spring. The community then began to wane irregularly through to the autumn when less than 1,000 cells cm^{-2} occurred on the rocks. Seasonal changes in the standing crop in terms of volume almost exactly paralleled those outlined above, with the highest values for 1973 and 1974 being 1.8×10^{9} and 1.0×10^{9} μm^{3} cm^{-2} respectively.

The greatest daily rate of recruitment exhibited by the community, 3.67×10^{4} cells cm^{-2}, took place during March 1974 while relatively high levels, i.e. 3.00×10^{4}, 2.90×10^{4} and 2.67×10^{4} cells cm^{-2}, were also observed in May 1974 and in August and June of 1973 respectively (Fig. 6). The periods of maximum growth, when expressed in terms of cell volume, paralleled those described for numbers. The greatest daily value, 5.7×10^{7} μm^{3} cm^{-2}, was achieved in March 1974, followed by 5.0×10^{7} μm^{3} cm^{-2} in August 1973 and 3.3×10^{7} μm^{3} cm^{-2} in May 1973. Algae disappeared from the rocks at a maximum daily rate of 6.25×10^{4} cells cm^{-2}, while high levels, i.e. 4.33×10^{4}, 2.00×10^{4} and 1.45×10^{4} cells cm^{-2}, also occurred in May 1974, June 1974 and November 1973 respectively (Fig. 6). In terms of cell volume, the greatest daily disappearance rates, 3.25×10^{7}, 2.90×10^{7} and 2.17×10^{9} μm^{3} cm^{-2} were observed in October 1973, April and May 1974 and November and December 1973 respectively.

Potamoplankton and Planktonic Communities

Approximately 250 different kinds of algae occurred in the potamoplankton/plankton of the Avon River, most of which were also found in the epipelic and epilithic communities. Diatoms once again predominated with over 200 taxa followed by the chlorophytes with 20 forms, the cyanophytes with 14, the euglenoids with eight and the chrysophyta with two. _Stephanodiscus hantzschii_ was the most common diatom followed in much reduced numbers by _Achnanthes lanceolata_, _A. minutissima_ v. _cryptocephala_ and _Cocconeis placentula_ v. _euglypta_.

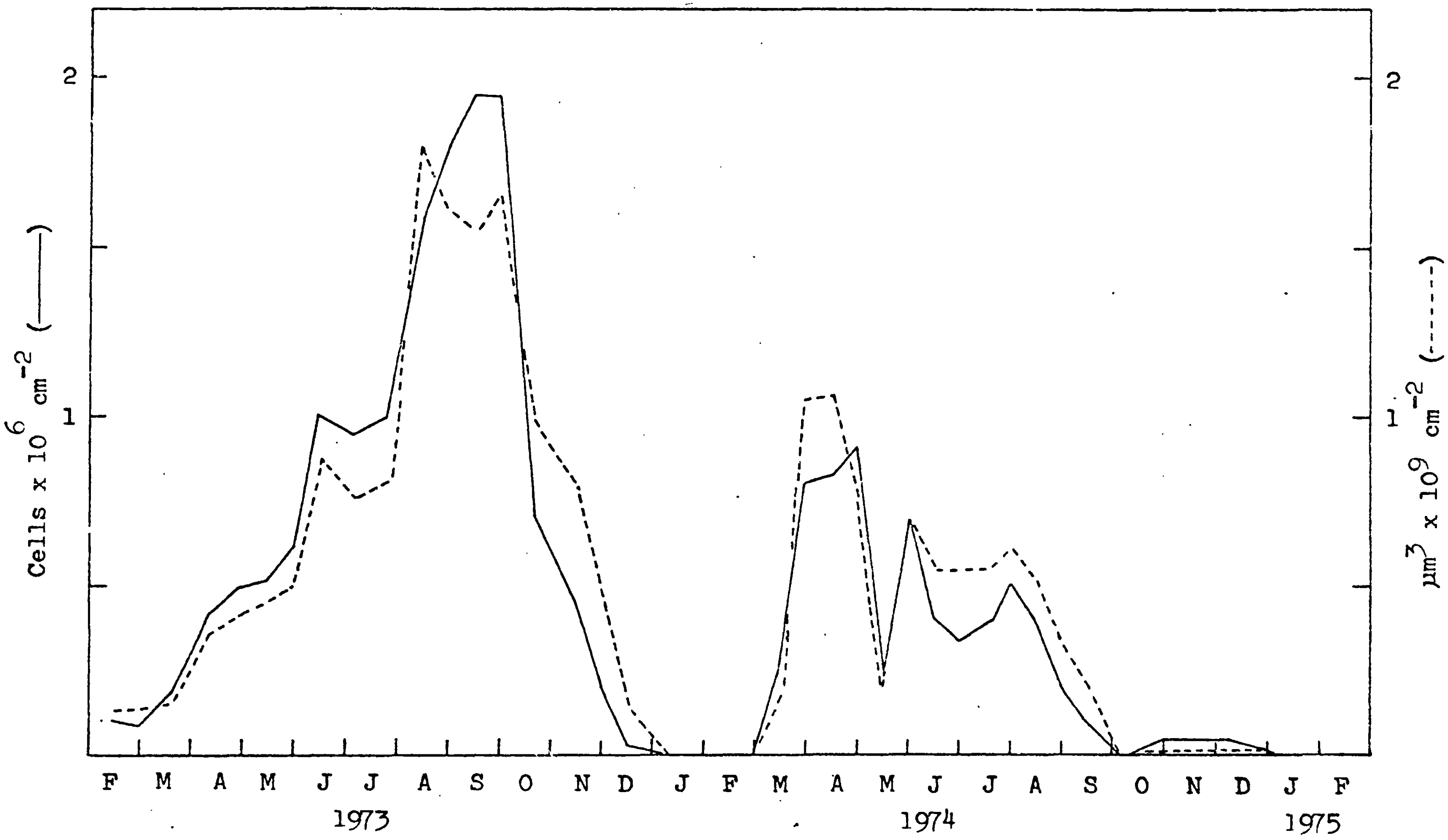

Fig. 6. Seasonal changes in the standing crop of the entire epilithic assemblage in the Avon River.

(Table 4, Fig. 7). While the predominant member of the Chlorophyta was always Chlamydomonas monadina, Scenedesmus dimorphus and S. quadricauda v. parvus also occurred abundantly on occasion. The Cyanophyta, Euglenophyta and Chrysophyta, represented mainly by Oscillatoria limosa, Euglena sp. and Dinobryon sertularia respectively, invariably maintained relatively small numbers.

The population of Stephanodiscus hantzschii expanded gradually during the first part of the investigation reaching a density of 1.10×10^7 cells l^{-1} near the first of July but subsequently waned more or less continuously to 1,000 cells l^{-1} by September (Fig. 7). After the overwintering period in which low standing crops prevailed, a well-defined bloom in the abundance of this species took place with numbers increasing from near zero to 3.56×10^7 cells l^{-1} near the beginning of May 1974. Thereafter, however, the population declined rapidly, falling to 8×10^5 cells l^{-1} by the late summer. Chlamydomonas monadina maintained a comparatively small population, 4×10^4 cells l^{-1}, during the initial stages of the investigation but showed a sharp rise in abundance near the middle of September when a standing crop of 1.13×10^6 cells l^{-1} was observed. Apart from a small bloom during December, the density of this species subsequently remained low until the spring of 1974. The population then began to expand, attaining maximum abundance, 9.75×10^5 cells l^{-1}, near the middle of September. Both Achnanthes lanceolata and A. minutissima v. cryptocephala occurred in small numbers, i.e. less than 2.7×10^5 cells l^{-1}, for most of the investigation but during May 1974 densities as high as 1.9×10^6 cells l^{-1} were recorded for both species.

The total number of algae floating in the water (i.e. true plankton and potamoplankton) increased more or less uniformly during 1973 with a maximum density of approximately 12×10^6 cells l^{-1} developing at the beginning of July (Fig. 8). Thereafter, the community decreased in numbers dramatically showing only a few periods of significant growth. A sharp rise in abundance took place during April and May of 1974 when a maximum standing crop of 48.4×10^6 cells l^{-1} was observed . Once again , however, numbers subsequently decreased with only 2.0×10^5 cells l^{-1} present during August. Seasonal changes in the standing crop of the flora in terms of cell volume almost exactly paralleled those outlined for numbers (Fig. 8). The

Table 4a. List of algae floating in the Avon River which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Achnanthes minutissima v. *cryptocephala*
Cocconeis placentula v. *euglypta*
Cyclotella meneghiniana
Fragilaria capucina v. *lanceolata*
Nitzschia acicularis
Stephanodiscus hantzschii
Chlamydomonas monadina
Scenedesmus dimorphus
Scenedesmus quadricauda v. *parva*

Table 4b. List of planktonic algae collected from the Avon River which accounted for between 1 and 10% of the flora on at least one sampling date.

Cyclotella stelligera
Cyclotella stelligera v. *tenuis*
Chlamydomonas sp.
Oocystis sp.
Pediastrum duplex
Scenedesmus bijuga
Scenedesmus quadricauda
Selenastrum gracile

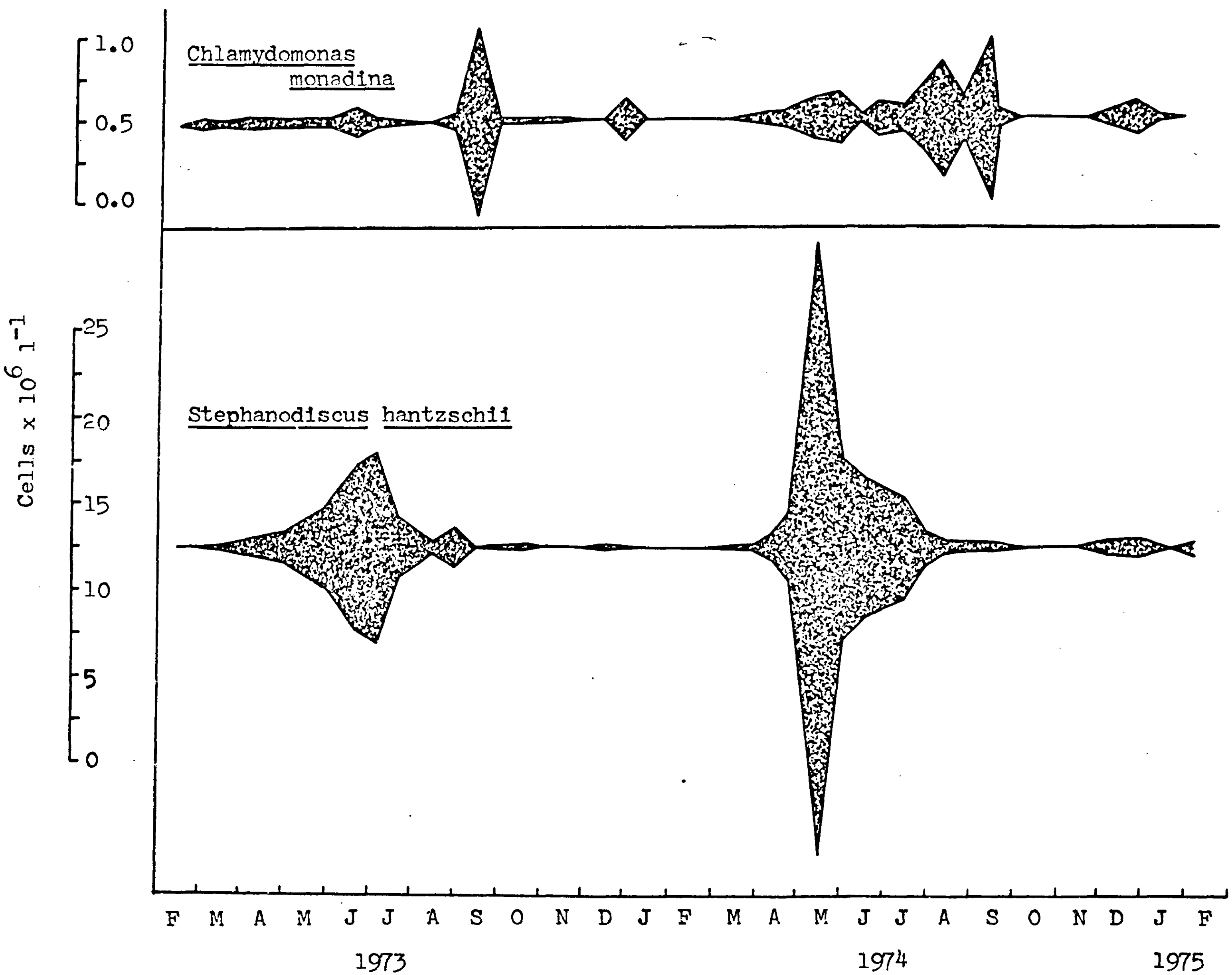

Fig. 7. Seasonal changes in the standing crop of common algae floating in the Avcn River.

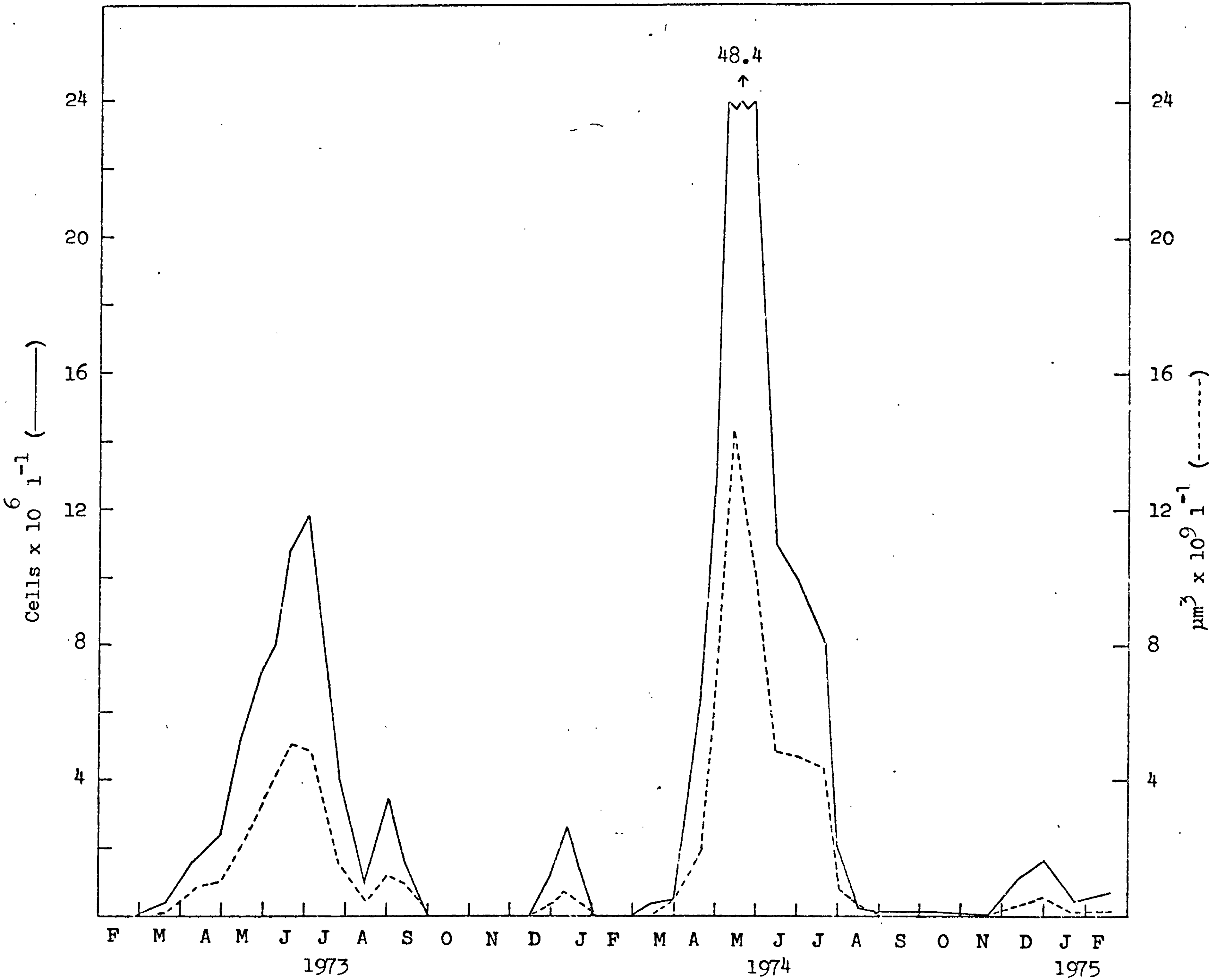

Fig. 8. Seasonal changes in the standing crop of the entire algal assemblage floating in the Avon River.

greatest amount of algae recorded during 1973 was 4.9×10^9 $\mu m^3\ l^{-1}$ while the corresponding value for 1974 was 14.4×10^9 $\mu m^3\ l^{-1}$. The fastest daily rate of recruitment into plankton, 2.37×10^6 cells l^{-1}, occurred during May 1974 and relatively high values, i.e. 6.3×10^5, 3.0×10^5 cells l^{-1}, were also observed during April 1974 (Fig. 8). In terms of cell volume, the periods of maximum daily recruitment were identical to those outlined above with a maximum value of 5.86×10^8 $\mu m^3\ l^{-1}$ being recorded.

Epiphytic Communities

The standing crop of Cladophora, estimated from the scrapings of five rocks of 5 – 20 cm diameter taken from each area where the epipelic algae were collected, increased from low levels, 0.005 g m^{-2} in March 1973 to 0.2 g m^{-2} in September of the same year before then falling sharply in the winter (Fig. 9). During March of 1974, the standing crop increased again and a maximum value of 0.14 g m^{-2} was recorded near the beginning of July.

Approximately 150 algal taxa were found in association with Cladophora, of which 118 belonged to the Bacillariophyta, 20 to the Chlorophyta, seven to the Cyanophyta and at least five to the Euglenophyta. Rhoicosphenia curvata, Diatoma vulgare and varieties, Melosira varians, Cocconeis pediculus and C. placentula v. euglypta were the predominant members of the first algal group while Scenedesmus quadricauda and S. quadricauda v. parvus were the most common chlorophytes (Fig. 10). Chamaesiphon incrustans accounted for the majority of the cyanophytes and Trachelomonas volvocina was predominant among the Euglenophyta.

The abundance of major epiphytic algae showed dramatic differences between the two years (Fig. 10). Rhoicosphenia curvata, for example, occurred abundantly during most of 1973 attaining its maximum density of 5.0×10^7 cells g^{-1} dry weight of Cladophora in June. During 1974, however, the population remained highly restricted with maximum development, 1.8×10^7 cells g^{-1}, taking place near the beginning of August. Similarly, Diatoma vulgare and D. vulgare v. producta occurred in relatively low abundance throughout most of the investigation but showed a tremendous increase in numbers to 1.09×10^8 and 0.98×10^8 cells g^{-1} respectively during April 1974. Both Cocconeis

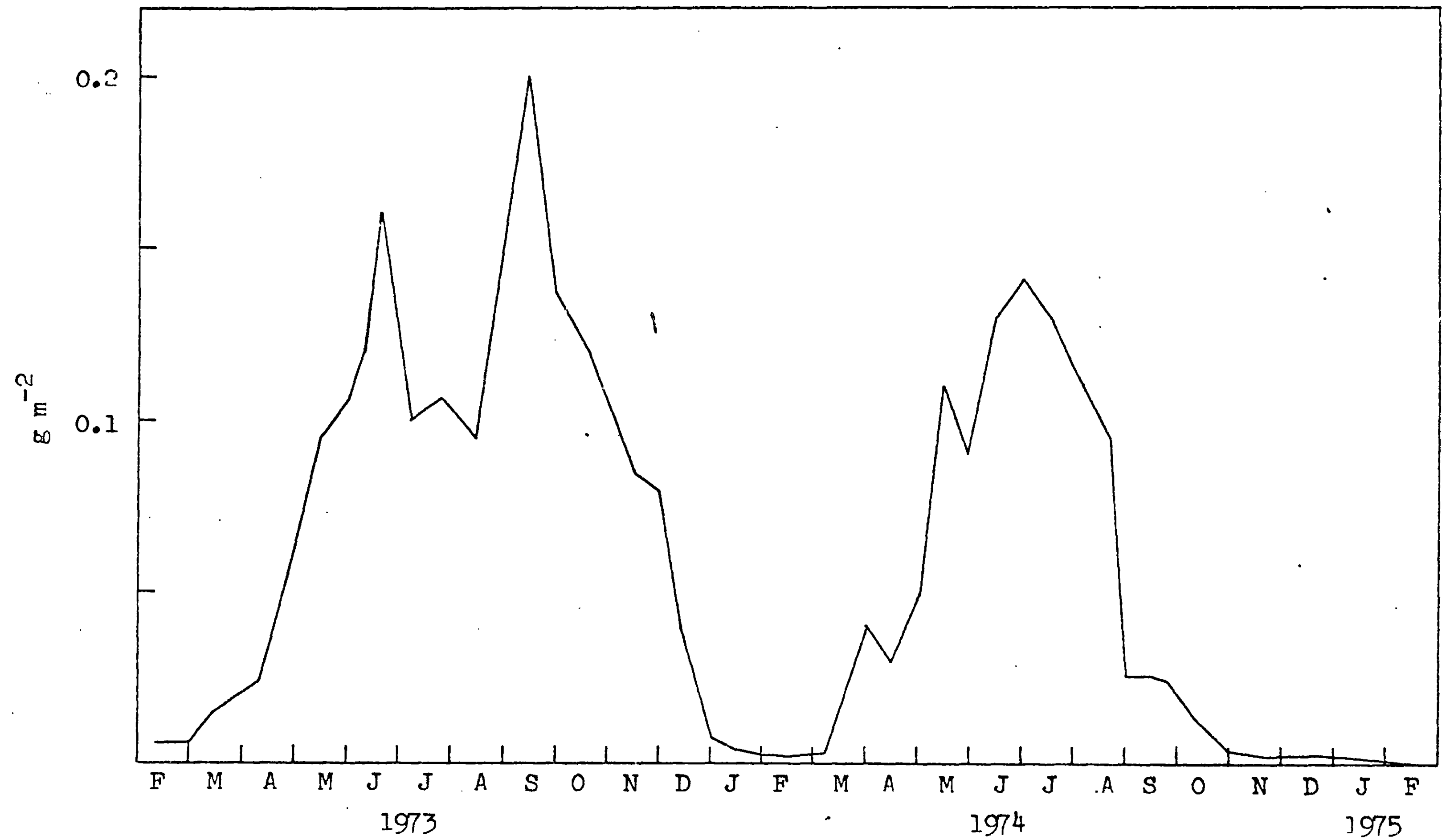

Fig. 9. Seasonal changes in the dry weight of Cladophora glomerata attached to rocks in the Avon River.

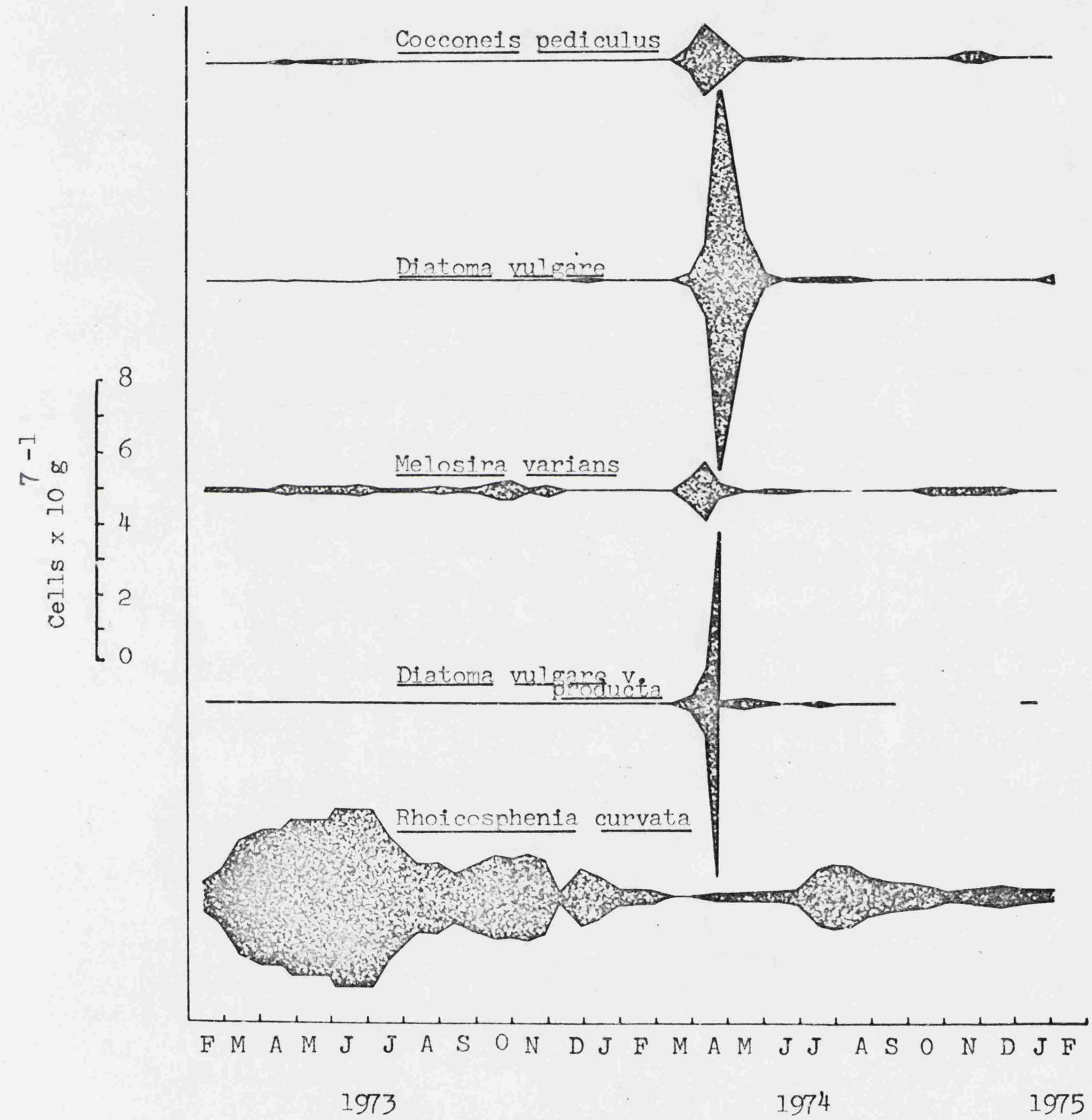

Fig. 10. Seasonal changes in the standing crop of common algae epiphytic upon *Cladophora glomerata* in the Avon River,

pediculus and to a lesser extent Melosira varians, although normally rare, exhibited well-defined peaks at only one time during the investigation.

The total standing crop of the epiphytic flora increased sharply during February and March 1973 and reached a maximum value of approximately 62 x 10^6 cells g^{-1} dry weight of Cladophora near the end of June (Fig. 11). The density of the algae subsequently declined quickly but recovered to 10 x 10^6 cells g^{-1} in November only to fall to less than 2 x 10^6 cells g^{-1} in February coincident with severe flooding. The population then expanded tremendously attaining 252 x 10^6 cells g^{-1} near the end of April but thereafter decreased to 13 x 10^6 cells g^{-1} in June and subsequently remained at relatively low levels until the end of the investigation. Seasonal changes in the density of the flora when expressed in terms of cell volume almost exactly paralleled those outlined above, with the highest value, 200 μm^3 x 10^9 g^{-1} , being recorded in April 1974 (Fig. 11).

The number of epiphytes associated with Cladophora increased on a daily basis most rapidly towards the end of April 1974 when a value of 10.8 x 10^6 cells g^{-1} was recorded (Fig. 11). The second fastest rate, 5.9 x 10^6 cells g^{-1}, occurred near the beginning of the same month while the highest value recorded during 1973, 1.67 x 10^9 cells g^{-1}, also took place in April. In terms of cell volume, the periods of maximum daily growth were identical to those outlined above, the highest level being 8.33 x 10^9 μm^3 g^{-1}. Algae disappeared from Cladophora at maximum daily rates of 10.8 x 10^6 and 1.93 x 10^6 cells g^{-1} during May 1974 and December 1973 respectively, while the corresponding levels in terms of cell volume were 9.0 x 10^9 and 1.4 x 10^9 μm^3 g^{-1} (Fig. 11).

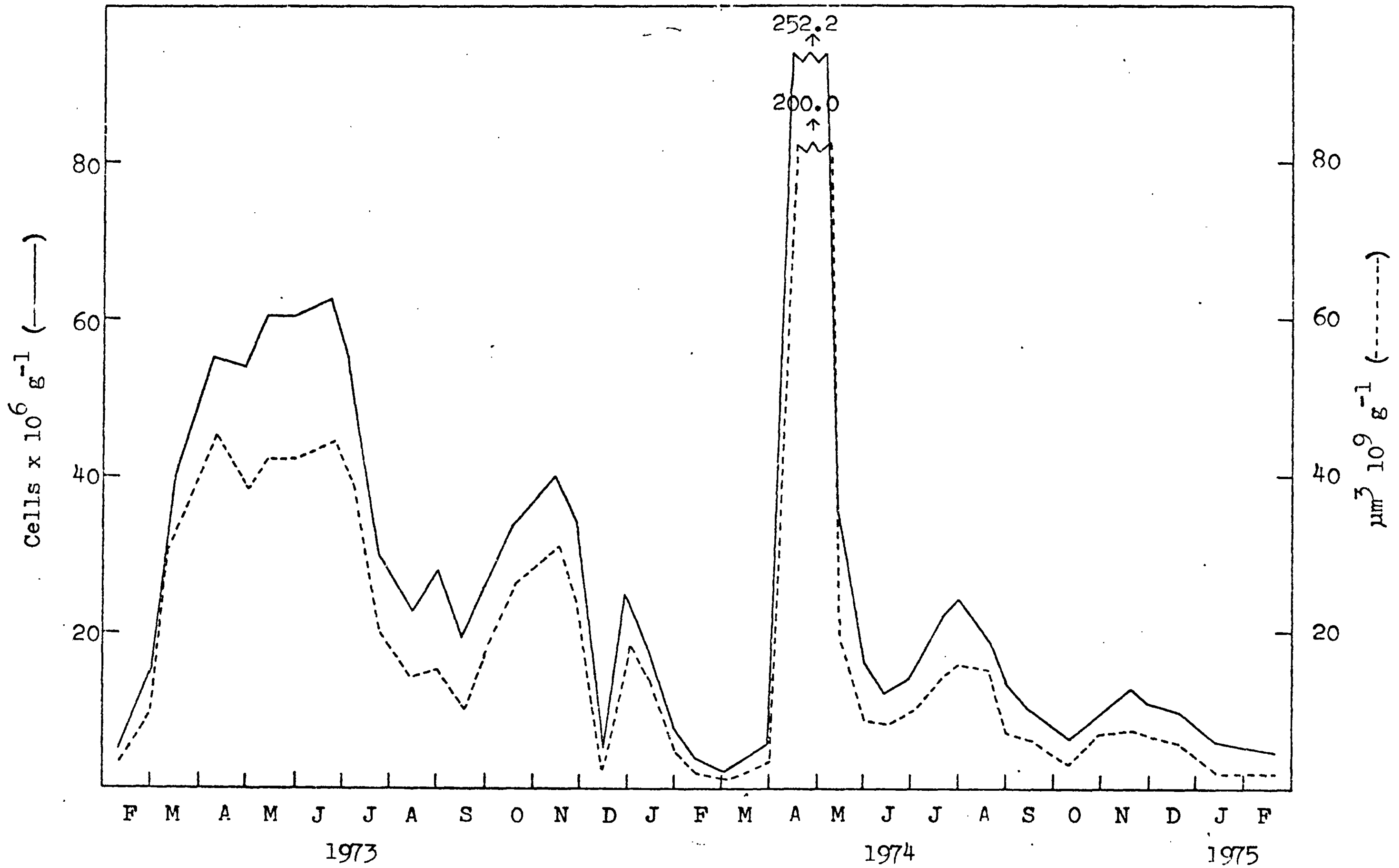

Fig. 11. Seasonal changes in the standing crop of the entire algal assemblage epiphytic upon *Cladophora glomerata* in the Avon River.

Discussion

The fact that the total standing crop of the epipelic flora in the Avon increased greatly during March of both years, paralleling the situation recorded in several other studies in the British Isles (Butcher *et al*., 1937; Round, 1960, 1961; Moss and Round, 1967) indicates that the level of at least one environmental parameter passes through a critical point at this time of the year. Since day length increased rapidly, while nutrient levels and temperature remained relatively constant, at least in 1973, it appears that the former parameter is probably primarily responsible for the onset of the spring bloom. This view is in agreement with the observations of Reynolds (1973) who worked on planktonic communities in small lakes. Furthermore, highly consistent patterns of seasonal succession for diatom communities have been recorded in a thermal spring where the environment was, apart from light, essentially homogeneous throughout the year (Stockner, 1968). Most of the more common species in the spring bloom, e.g. *Surirella ovata* v. *minuta*, *Navicula viridula* v. *minor*, *Nitzschia acicularis*, *N. linearis* and *N. palea*, were the same as those given by Butcher (1932), Rice (1938) and Round (1972) for other areas in England. Since minor fluctuations in environmental conditions are unlikely to limit the growth of all these species, the presence of a relatively large pool of common taxa may be the reason why epipelic communities in many areas have the capacity almost always to expand greatly at about this time each year.

In this study it was perhaps unexpected to find that, especially in view of the exceptionally high growth rates exhibited in late March and April, the epipelic algal population showed no increase in numbers between the floods of May and July 1973. This feature can probably be explained by the fact that during this period the large population of planktonic diatoms, mainly *Stephanodiscus hantzschii*, reduced the level of SiO_2 from 9.5 to 0.5 - 1.0 mg l^{-1}, a pattern noted in other areas at a comparable time of the year (Edwards, 1969; Wang and Evans, 1969). Thus since other nutrients, as well as temperature and light, remained at adequate levels at this time, expansion of the epipelic community may have been restricted by the reduction in available silicon. If this is the case, then the question arises as to why, in contrast to the epipelic community, the planktonic algae were able to recover so rapidly from the floods. For example, even if the planktonic algae were able to compete more successfully for silicon than the benthic forms, an initial and dramatic expansion of the epipelic community would be expected. It is possible that for some reason the scouring effect of the floods had significantly altered, on a relatively long term basis, the microhabitat of benthic algae. The above views on silicon depletion and alteration of microhabitat are further supported by the observation that considerable development of the epipelic community took place during August, coincident with an extended period of low water and a sharp reduction in the density of planktonic algae.

It was surprising to find during 1973 a bloom in the epipelic flora in early December, at a time when light intensity and duration were low and when no elevations in silicon, nitrogen and phosphorus could be detected. At present one can only suggest that during this time unmeasured nutrients had increased to a relatively higher level, a situation that could not through the effects of flooding have been observed during the same time in 1974.

The timing and the magnitude of the spring bloom in 1974 roughly paralleled that recorded in the previous year and no significant change took place in the species composition of the predominant algae. Although the abundance of several of these epipelic taxa varied greatly between the two years, no clear difference in environmental parameters could be found to account for these differences in numbers. In contrast to 1973, the standing crop of the entire community in 1974 decreased during the remainder of the summer, a feature apparently related to the absence of scouring of the river bed and paralleling the situation found in comparable communities in several different parts of the world (Brook, 1955; Dor, 1970). One possible way in which the absence of flooding had reduced the quality of the environment in 1974 is through the large number of algae on the sediments causing a significant deterioration in the components of the sediment surface through such factors as mechanical disruption, production of growth inhibiting metabolic end products and the exhaustion of at least one important nutrient (Round, 1957). Presumably, the scouring action of floods would totally destroy this highly modified and possibly depleted microhabitat and at the same time permit the development of a more suitable substrate.

In contrast to the epipelic flora, the elucidation of patterns of change in the standing crop of the epilithic flora is complicated by the fact that a well-defined spring bloom occurred only in 1974. Since the epipelic community in the Avon exhibited considerable expansion during the spring of 1973, growth conditions such as light, temperature and nutrient supply, were presumably not responsible for the restricted bloom of the epilithic forms at this time. Furthermore, since the predominant species in terms of relative abundance on the rocks were, for the most part, similar to those living on the sediments, any complicated interaction of environmental parameters on growth should also have been exhibited in the epipelic community. A reason for the discrepancy between the two years may be due to differences in water velocity over the rocks, i.e. 18 cm sec^{-1} in 1973 compared with 6 - 7 cm sec^{-1} in 1974. Since the predominant species early in the bloom of 1974, Navicula viridula v. minor, apparently has only small adhesive powers, part of the population would have probably been scoured away at this time in 1973. Although Diatoma vulgare was by far the most important species later in the 1974 bloom, this taxon also failed to develop a significant population during the same period in 1973, a feature undoubtedly due to the extensive flooding at this time. In other words, apparently either faster flow rates or very heavy flooding can have a destructive effect on the population of key epilithic species at the time when they are about to show substantial increase in numbers.

The maximum development of the epilithic flora between August and September 1973 contrasts with the situation found at the same time in 1974 when a relatively small population was observed. This feature is apparently correlated with the fact that in the former year the period of high standing crop followed high water levels whereas in the latter the discharge rate was low throughout the summer. It thus appears that, as with the epipelic community, the scouring action of the floods, following periods of rapid growth, can lead to an enhancement of the quality of the substrate surface. The communities differ, however, in the time delay between the period of flooding and a significant expansion in the community, this being considerably longer in the epipelic flora. It would thus appear that flooding has comparatively less effect on the microhabitat of the epilithic flora, presumably because of the relatively more solid nature of the substrate.

Although, since the estimates of standing crop in the Avon River plankton do not take into consideration the dilution effect of high water periods in 1973, the relative constancy of discharge through much of 1974 enables an accurate assessement of seasonal changes in the number of algae. During this year, the population of the predominant planktonic genus, Stephanodiscus, rose sharply from very low levels in the first half of April to peak values of 3.56×10^7 cells l^{-1} in May, paralleling a similar but not as dramatic pattern in the rivers examined by Swale (1964) and Lack (1971). Since, during March of 1974, S. hantzschii did not exhibit the characteristic upsurge of benthic species particularly apparent in the epipelic communities, and as temperature was unlikely to have been limiting (Swale, 1963; Lack, 1971), it seems likely that the level of illumination was the factor restricting the growth rate at this time of the year. The absence during 1973 of a well defined upsurge in the numbers of Stephanodiscus is presumably related both to the high discharge rates and to the consequent dilution factor caused by the frequent flooding. In contrast to their maximum abundance in July of 1973, the greatest density of Stephanodiscus on the sediments was observed during the middle of August, approximately one and a half months after the bloom in the plankton. This may be attributable to a loss of ability by the algae to stay afloat during the late summer and autumn, a feature which may in turn be related to the utilization of lipid. Although the peaks of Stephanodiscus in both the plankton and benthos occurred at the same time in 1974, it should be noted that the apparent large scale deposition on the substrate of several other species did occur in local still water populations.

In both years, Chlamydomonas monadina occurred most abundantly in either August or September, several months after the Stephanodiscus bloom, contrary to the findings of Swale (1969) and Hickman (1974a) who reported this species usually achieves greatest development early in the summer. Similarly Lack (1971) reported that an unidentified species of Chlamydomonas was observed most frequently during June. Since the large population of Stephanodiscus found in May and June of both years in the Avon did not, apart from silicon, deplete the nutrients, it seems likely that some factor other than nutrient supply, light or temperature had restricted the flora.

Although tremendous expansion of the flora associated with Cladophora glomerata occurred during March 1973 coincident with a similar increase in the epipelic community, the standing crop of the epiphytes subsequently remained high, despite the fact that there was frequent flooding. This is almost certainly due to the fact that, since the predominant species at this time, Rhoicosphenia curvata, often occurs in fast flowing water (Appendix 1), there is unlikely to be any major detachment, a situation which Douglas (1958) has suggested might also be the situation in the case of other epiphytic diatoms. As with many other algal communities in this and other studies (e.g. Hickman, 1974a), the flora epiphytic upon Cladophora exhibited a sharp decline in numbers in the continual absence of flooding.

The density of Rhoicosphenia curvata during the spring bloom of 1974 remained low compared to the values recorded in 1973, reflecting the inability of this species to grow well in the relatively slow flowing water at this time. The numbers of Diatoma vulgare and D. vulgare v. producta in 1974, on the other hand, were much higher than in the previous year, a feature presumably related to the absence of competition from R. curvata. The subsequent sharp fall in the density of Diatoma is almost certainly due to the large scale detachment that takes place at times when photosynthetic rates are unusually high (see below).

That the maximum rate of growth exhibited by the epipelic, epilithic, planktonic and epiphytic communities occurred during the spring of 1974 indicates that there is considerable similarity in the factors controlling increases in these populations. Although the highest rates at which algae disappeared from the sediments and rocks were recorded during severe flooding, only slightly lower levels occurred during May 1974 when there was a sustained period of low water. The predominant species disappearing from the epipelic assemblage at this latter time were *Navicula viridula* v. *minor*, *Nitzschia* spp., and *Surirella ovata* v. *minuta* while *N. viridula* v. *minor* was the only major form on the rocks. Since it is doubtful that all of these species could wane so suddenly leaving only an insignificant population behind, it seems likely that another factor is primarily responsible for the large scale detachment. Blum (1954) and Müller-Haeckel (1966) have suggested that at least some species of algae become detached from the substrate near mid-day and subsequently appear in the plankton, a feature correlated with high photosynthetic activity. In the present study, all the species which exhibited a dramatic fall in numbers had, in the immediately prior period, been exhibiting unusually quick growth. It therefore seems likely that environmental conditions were well suited for high levels of photosynthesis which in turn may have caused the large scale detachment of the algae. A similar pattern almost certainly occurred during May 1974 in the epiphytic assemblage when *Diatoma vulgare* and *D. vulgare* v. *producta* disappeared abruptly.

Highland Water

Highland Water is 10 km in length falling approximately 80 m from its source to the Lymington River. For most of its length, the stream drains lightly forested land, the New Forest, which supports a limited amount of grazing. Epipelic algae were collected from three sites (Lat. 50° 52' , Long. 1° 37') located within 0.5 km of one another. Most of the stream at this point was well shaded with trees and its width was 2 - 4 m. Samples of epilithic and planktonic algae were also collected at the same location from four and two sites respectively.

Physico-chemical Analyses

Water temperatures at all sites increased more or less continuously from about $1^{\circ}C$ in March 1973 to 15 - $16^{\circ}C$ in September before falling to values of between 1 and $7^{\circ}C$ during the following winter (Fig. 12). A similar pattern was followed in 1974 although the minimum values did tend to be rather higher than in 1973. The highest discharge rates, 3 - 4 m^3 sec^{-1}, occurred during the winter floods while the lowest, 0.003 m^3 sec^{-1}, were invariably observed during the summer. Water velocity over the epipelic collection sites averaged from 2 to 20 cm sec^{-1} during the warmer months but occasionally rose to at least 50 cm sec^{-1} during January and February (Fig. 12). The water depth at these stations also fluctuated seasonally averaging, during the summer, 3 - 4 cm at Site A and 10 - 12 cm at Sites B and C while in the winter the respective values at these sites were 7 - 9 and 15 - 20 cm. The rate of water flow over the four epilithic collection areas, subsequently referred to as Sites I,II,III and IV, normally varied between 30 and 60 cm sec^{-1}, depending on the site, and the water depth remained relatively constant at 7 - 11 cm. Highland Water was usually slightly acidic and no consistent pattern of seasonal variation was observed in the amount of nutrients in the water (Table 5). The organic content of the sediment averaged 9.5% with maximum and minimum values of 16 and 3% respectively. Light intensity at the surface of the water was higher during the winter at mid-day (150 lux) than in the summer (100 lux) reflecting the effect of shading by the canopy of leaves.

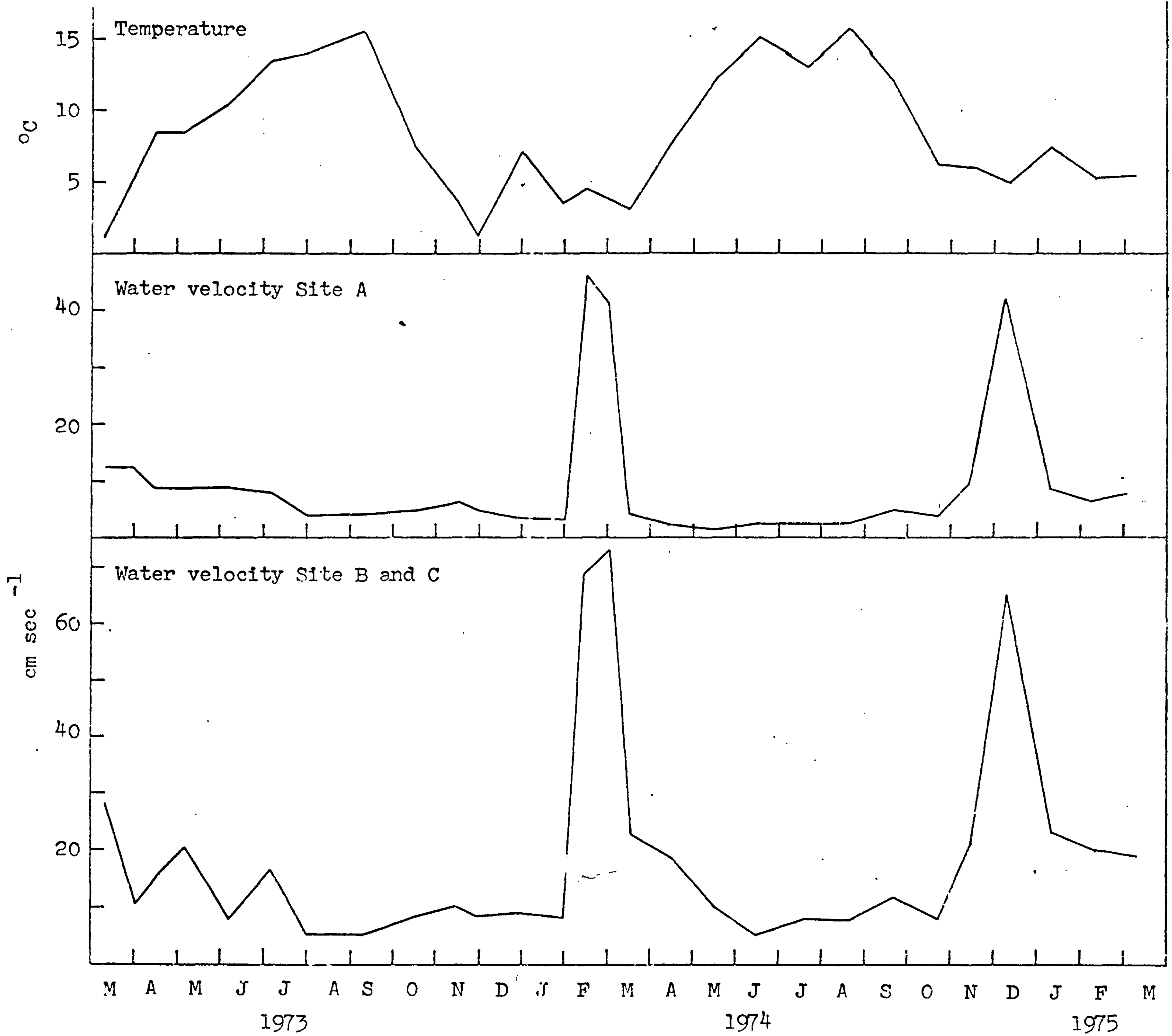

Fig. 12 Seasonal changes in the temperature of Highland Water together with the water velocity over the epipelic collection sites.

Table 5. Physico-chemical properties of water from Highland Water during 1973 and 1974. Except for pH, all data are expressed in terms of mg l^{-1}.

Parameter	Average	Range
pH	6.9	6.6 - 7.2
Total Alkalinity	25	18 - 44
Silica	5.7	3.5 - 7.8
Orthophosphate-Phosphorus	0.07	0.008 - 0.10
Nitrate-Nitrogen	0.75	0.35 - 1.2

Epipelic Communities

A total of 152 species of algae were collected from the sediments of Highland Water of which 134 belonged to the Bacillariophyta. The predominant taxa in this group were Achnanthes minutissima v. cryptocephala, A. saxonica, Cymbella naviculiformis, Opephora martyi, Pinnularia biceps and varieties, P. viridis and Synedra ulna and varieties (Table 6, Fig. 13). The Cyanophyta were occasionally well represented by Oscillatoria geminata and Aphanothece sp. , while an unidentified species of Chlamydomonas was the only frequently encountered member of the Chlorophyta. The other major groups of algae were seldom if ever encountered in the stream.

Although recurring patterns of seasonal changes in density were usually observed in all the common species, large differences in the abundance of these algae were also found between the two years. For example, Achnanthes minutissima v. cryptocephala, the most common alga on the sediments, was found in relatively large numbers during both summers but the maximum standing crop in 1973, 2.35×10^5 cells cm^{-2}, far exceeded that of 1974, i.e. 4.0×10^4 cells cm^{-2} (Fig. 13). Much the same pattern of succession was observed for Achnanthes saxonica with maximum standing crops of 1.8×10^5 and 3.0×10^4 cells cm^{-2} respectively. Cymbella naviculiformis, on the other hand, reached maximum development during April in 1973 and during May in 1974. The standing crop at these times was 1.65×10^5 and 0.4×10^5 cells cm^{-2}, respectively, with values decreasing to about 0.5×10^4 cells cm^{-2} during the autumn and winter of both years. Unlike the other diatoms, Opephora martyi reached densities of 5.5×10^4 cells cm^{-2} between March and May 1973 but thereafter never appeared in large numbers.

Pinnularia biceps and P. biceps f. petersenii, which invariably occurred in a ratio of 2.5 - 3:1 throughout the investigation were the most frequently encountered algae on the sediments during both winters with an average standing crop of 1.18×10^4 cells cm^{-2}. Their greatest density (8.04×10^4 cells cm^{-2}), however, occurred during May 1974, the numbers during 1973 averaging considerably less (3.5×10^4 cells cm^{-2}). As with most other species, Synedra ulna showed much greater development during the summer of 1973 than in 1974. Blue-green algae; represented mainly by Oscillatoria geminata and Aphanothece sp. , occurred on the sediments throughout both years

Table 6. List of epipelic algae collected from Highland Water which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes minutissima v. *cryptocephala*

Achnanthes saxonica

Cymbella naviculiformis

Cymbella ventricosa

Eunotia curvata

Eunotia exigua

Fragilaria capucina v. *lanceolata*

Navicula cryptocephala

Navicula pupula v. *capitata*

Nitzschia linearis

Nitzschia palea

Opephora martyi

Pinnularia biceps

Pinnularia biceps f. *petersenii*

Pinnularia viridis

Stauroneis anceps

Synedra ulna

Synedra ulna v. *amphirhynchus*

Synedra ulna v. *danica*

Tabellaria flocculosa

Chlamydomonas sp.

Aphanothece sp.

Oscillatoria geminata

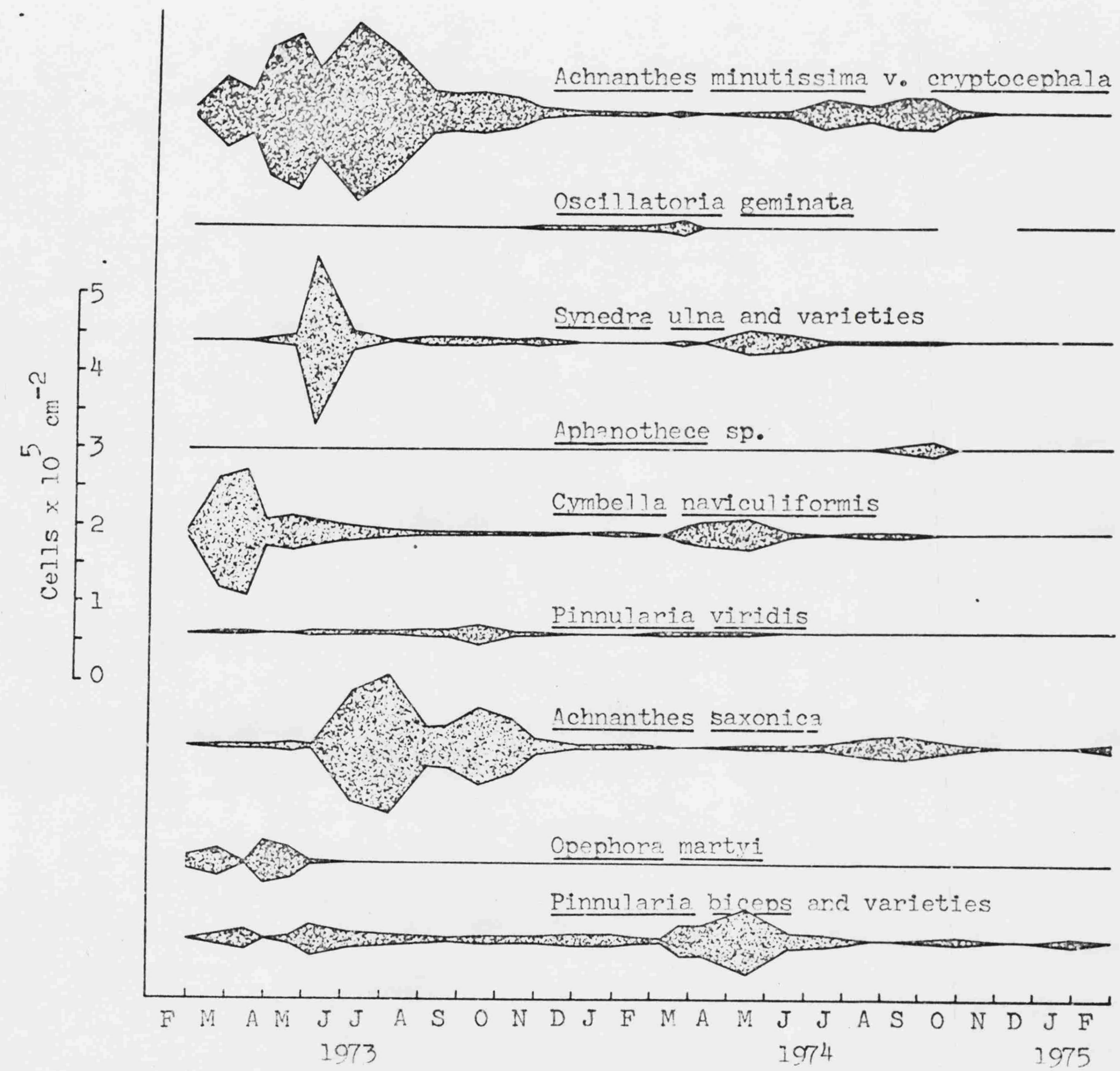

Fig. 13. Seasonal changes in the standing crop of common epipelic algae in Highland Water.

albeit in relatively low numbers. The former species was most frequently encountered between November 1973 and April 1974 when a maximum standing crop of 1.9×10^4 filaments cm^{-2} was recorded. In contrast Aphanothece did not appear abundantly until the fall of 1974. An unidentified species of Chlamydomonas, although normally rare or absent on the sediments, occurred abundantly during the middle of August 1974.

The total standing crop of the assemblage increased sharply to 6.8×10^5 cells cm^{-2} during March 1973 but subsequently fell to low levels in April only to rise again to 1.1×10^6 cells cm^{-2} near the beginning of July (Fig. 14). Thereafter, the community waned, failing to show any recovery until May 1974. Seasonal changes in the population during this latter year differed considerably from those outlined above with the maximum standing crop, 2.4×10^5 cells cm^{-2}, occurring towards the end of October. In terms of cell volume, significant expansion of the community began during May of both years but the highest standing crop was always observed in June.

The fastest daily growth rates in terms of numbers occurred during March and June 1973, when values of 3.0×10^4 and 1.4×10^4 cells cm^{-2} were recorded (Fig. 14). In terms of volume, however, maximum daily rates, i.e. 8.0×10^6 and 6.4×10^6 μm^3 cm^{-2}, were observed during May of 1973 and 1974 respectively, followed by June 1974 when a value of 3.7×10^6 μm^3 cm^{-2} was recorded. The fastest rates of disappearance of algae from the sediments, 2.33×10^4 and 1.35×10^4 cells cm^{-2}, took place during March and April 1973 and between July and September 1973 respectively, while in terms of volume the greatest daily rates, 6.14×10^6 and 2.88×10^6 μm^3 cm^{-2}, were recorded during June and July 1973 respectively (Fig. 14).

Epilithic Communities

A total of 109 different species, varieties and forms of algae were found in the epilithic communities of Highland Water and of these 98 were diatoms, seven were cyanophytes and four were chlorophytes. Achnanthes saxonica was often overwhelmingly predominant and frequently represented more than 90% of the algae. It was followed in order of descending abundance by Achnanthes minutissima v. cryptocephala, Gomphonema spp. and Synedra ulna v. amphirhynchus (Table 7). The most

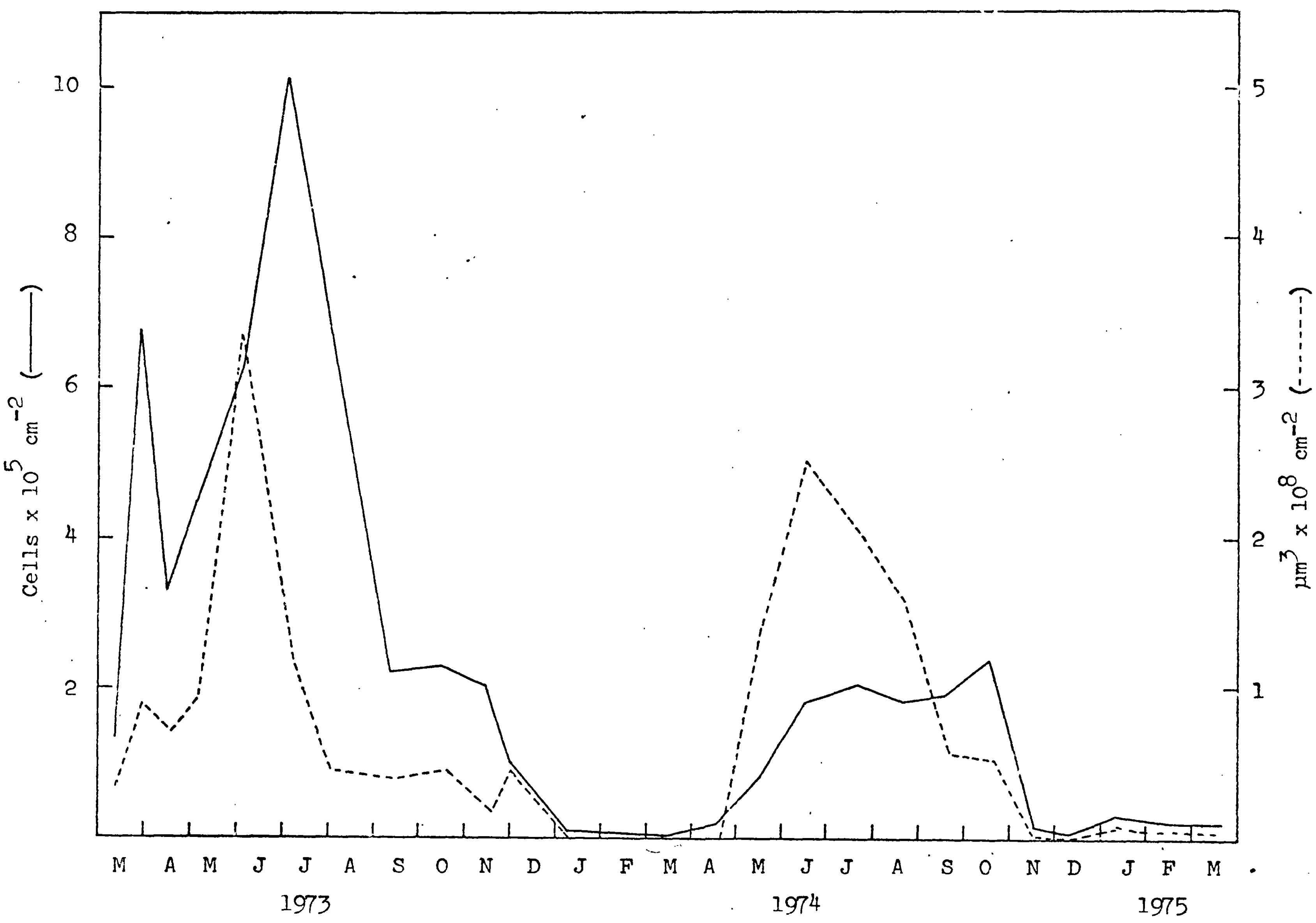

Fig. 14. Seasonal changes in the standing crop of the entire epipelic assemblage in Highland Water.

Table 7. List of epilithic algae collected from Highland Water which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes minutissima v. *cryptocephala*

Achnanthes saxonica

Eunotia curvata

Gomphonema acuminatum v. *coronatum*

Gomphonema constrictum v. *subcapitatum*

Navicula tripunctata

Nitzschia palea

Synedra ulna v. *amphirhynchus*

Mougeotia spp.

common cyanophyte was an unidentified species of Phormidium which seldom accounted for more than 0.1% of the algal flora. Sterile filaments of Mougeotia were the most frequently encountered representatives of the Chlorophyta but these forms seldom represented more than 0.1% of the algae although on one occasion at Site IV it rose to 22%.

Achnanthes saxonica was most common in collection areas I and II where the water velocity was relatively high, i.e. 55 - 60 cm sec^{-1} Normally this species represented more than 98% of the flora except when it fell to about 65% in the late summer of 1973, being partially replaced by Achnanthes minutissima v. cryptocephala, Gomphonema acuminatum v. coronatum, G. capitatum v.subcapitatum and Mougeotia sp. At Site III, where the water averaged 45 - 50 cm sec^{-1} , A. saxonica still accounted for at least 95% of the algae during most of the year although the level did fall to 70% during the summer of 1973 when A. minutissima v. cryptocephala showed an elevation in density. Considerable variation existed in the relative abundance of Achnanthes saxonica at Site IV where the water flowed at 30 - 40 cm sec^{-1}. For example, during the winter it constituted 98% of the algal flora but in the summer and autumn was partially replaced by other diatoms which accounted for between 45 and 80% of the community. Predominant forms in this latter group included Achnanthes minutissima v. cryptocephala, Gomphonema spp. , Eunotia spp. and Synedra ulna v. amphirhynchus.

The total standing crop of epilithic algae in terms of numbers at Sites I and II averaged 0.8×10^6 cells cm^{-2} during the spring and early summer of 1973 increasing to 1.2×10^6 cells cm^{-2} by September (Fig. 15). Thereafter, numbers decreased more or less uniformly until March 1974 when 0.08×10^6 cells cm^{-2} were observed. The density of the algae remained relatively low during the following summer but reached 0.95×10^6 cells cm^{-2} in October only to fall again to low overwintering levels. The pattern of seasonal change in algal volumes was in general the same as that described above. However, during August and September (1973) a sharp rise in the standing crop to 4.0 $\times 10^8$ μm^3 cm^{-2} was observed, reflecting the previously mentioned appearance of Mougeotia. Although changes in the density of the algae on the rocks at Sites III and IV were similar to those outlined for I, the trends,when expressed in terms of cell volume, exhibited several differences (Fig. 16). For example, the sharp rise in the amount of

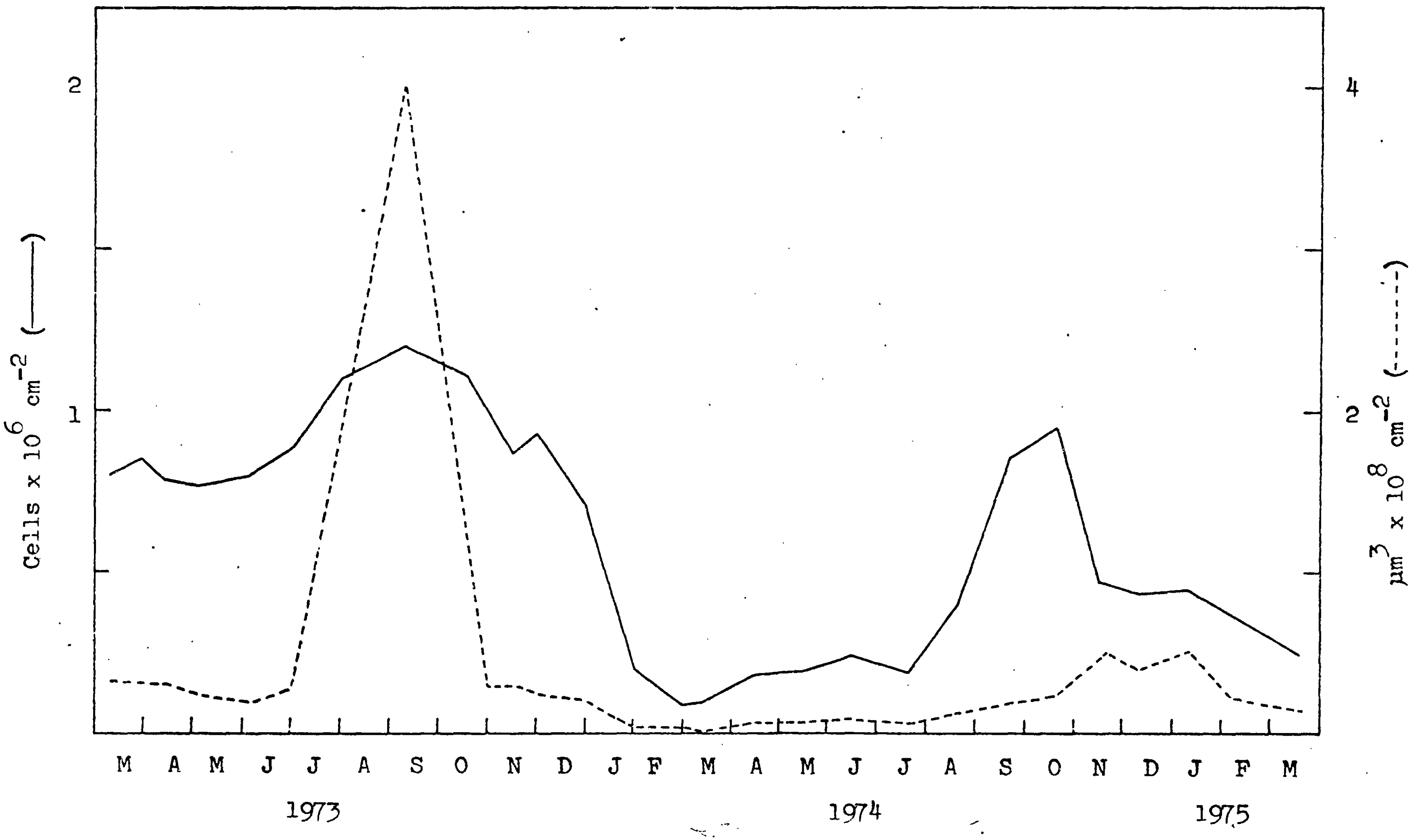

Fig. 15. Seasonal changes in the standing crop of the entire epilithic assemblage at sites I and II in Highland Water.

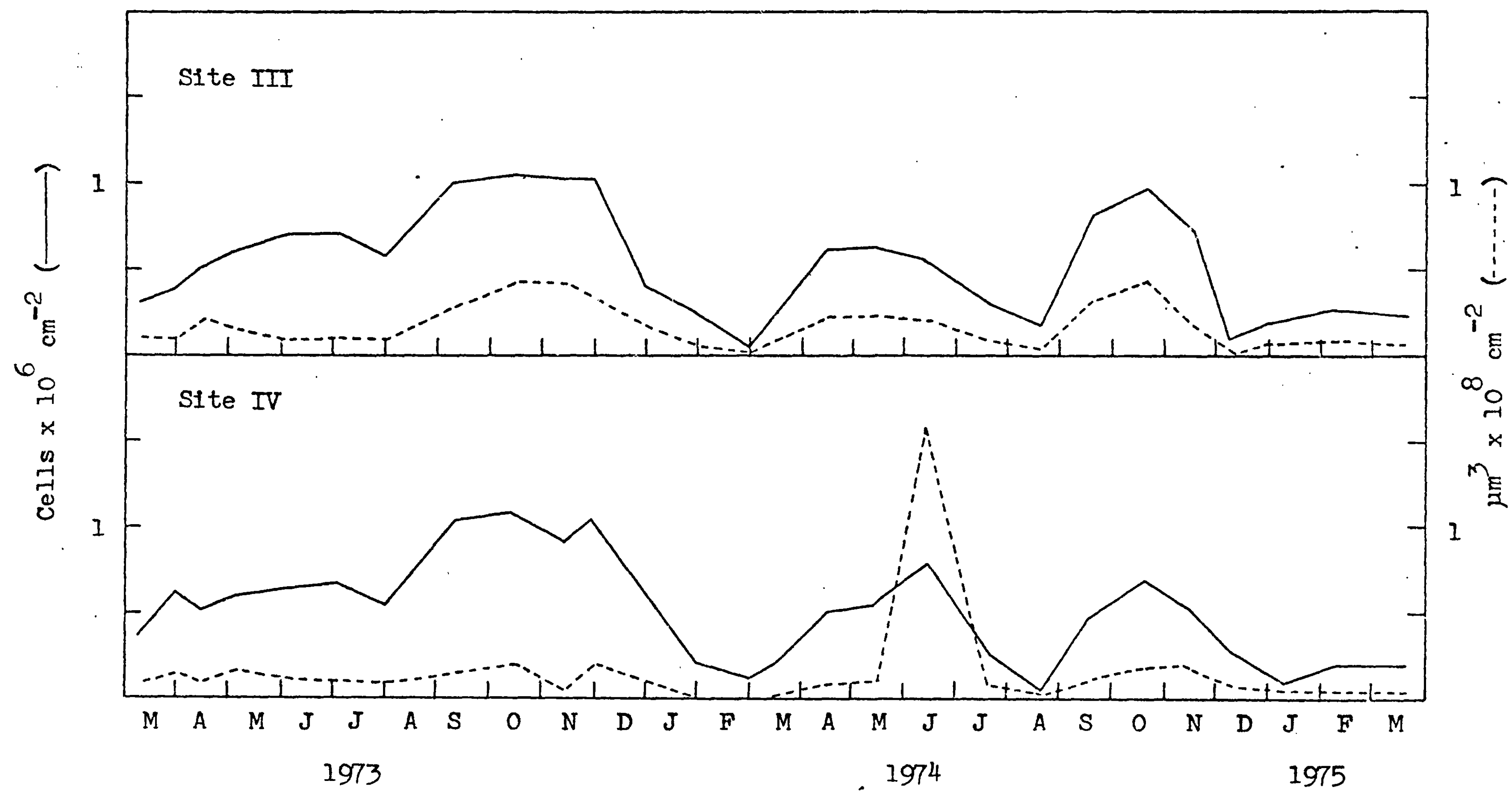

Fig. 16. Seasonal changes in the standing crop of the entire epilithic assemblage at sites III and and IV in Highland Water.

algae at I and II during August and September did not occur at III and IV. However, a significant rise in the standing crop to 1.6 x 10^8 μm^3 cm^{-2} was observed during June 1974 at Site IV, largely due to the increase in Synedra ulna v. amphirhynchus. This rise did not occur at Site III but the overall amount of algae was usually higher than at any other site.

The fastest daily growth rates in terms of numbers at all four sites occurred during September 1974 when values 1.5 x 10^4 and 2.1 x 10^4 cells cm^{-2} were recorded for areas I, II, IV and area III respectively (Figs 15,16). In terms of volume, however, a maximum daily rate of 5.29 x 10^6 μm^3 cm^{-2} was observed at Sites I and II between July and September 1973 (Fig. 15). Slower rates of algal development were found in areas II and IV where values of 1.01 x 10^6 and 3.30 x 10^6 μm^3 cm^{-2} day^{-1} were recorded in September 1974 and June 1974 respectively. The fastest daily rate of disappearance of living algae from the rocks at Sites I and II, 1.66 x 10^4 cells cm^{-2}, occurred during January 1974 while relatively high values of 0.90 - 0.95 x 10^4 cells cm^{-2} were also recorded in October and December of 1973. By far the greatest daily fall in terms of cell volume took place in the early autumn of 1973 when a value of 7.4 x 10^6 μm^3 cm^{-2} was observed. At Sites II and IV on the other hand, the greatest daily rate of disappearance by numbers, 1.4 - 2.2 x 10^4 cells cm^{-2}, occurred late in 1973 while comparatively high values were also found during June of 1974. The fastest daily decline in terms of volume at Site III, 5.33 x 10^5 μm^3 cm^{-2}, took place in December 1973 while the corresponding value in area IV, 2.0 x 10^6 μm^3 cm^{-2}, was observed in June and July of 1974.

Potamoplankton and Plankton Communities

A total of 164 different species, varieties and forms of algae were found floating in the water of the stream. One hundred and forty two taxa were diatoms while chlorophytes, cyanophytes and euglenoids were represented by ten, eight and four taxa respectively. There were, however, only about 20 species in the entire assemblage that could be considered as truly planktonic. The most common diatom species included Achnanthes saxonica, A. minutissima v. cryptocephala, A. lanceolata and Nitzschia palea, while the Chlorophyta was represented by Scenedesmus quadricauda , S. dimorphus and Chlamydomonas sp. (Table 8, Fig. 17). The only common cyanophyte was Aphanothece sp. and euglenoids were represented by only a few individuals of Trachelomonas volvocina and an unidentified species of Euglena.

The density of Achnanthes saxonica, although dropping to only 6.5×10^3 cells l^{-1} in April, generally increased during the spring and summer of 1973 reaching peak levels of 7.0×10^4 cells l^{-1} in July. Thereafter, numbers decreased sharply and, for the remainder of the study, never exceeded 1.0×10^3 cells l^{-1}. Changes in the abundance of Achnanthes lanceolata, A. minutissima v. cryptocephala and Cocconeis placentula v. euglypta followed a similar, but not as exaggerated a trend as that described above, with maximum standing crops of 1.4×10^4, 1.4×10^4, and 0.8×10^4 cells l^{-1} respectively. The pattern of succession exhibited by Rhoicosphenia curvata and Nitzschia palea, on the other hand, was characterized by two distinct peaks occurring during May and August, 1973 with relatively low densities being observed during the remainder of the study. The diatom Synedra ulna v. danica achieved greatest numbers (5.9×10^3 cells l^{-1}) early in August 1973 with high densities also occurring during the late spring and summer of 1974. The chlorophytes Scenedesmus quadricauda and S. dimorphus were frequently found during most of 1973 when densities of up to 7.5×10^3 cells l^{-1} were recorded but in 1974 the standing crop of these species was greatly reduced. In contrast the greatest numbers of Chlamydomonas ($5.0 - 7.6 \times 10^3$ cells l^{-1}) occurred during January and August 1974. The cyanophyte Aphanothece, although normally present in only small numbers, showed a marked but brief rise in abundance reaching 7.29×10^4 cells l^{-1} near the beginning of 1974.

The total number of algae in the water showed considerable variation during the study with distinct peaks occurring in all seasons (Fig. 18). Maximum algal densities, 16.5×10^4 cells l^{-1}, were observed during July 1973 while high values, $8 - 12 \times 10^4$ cells l^{-1}, were also recorded at the beginning of the investigation and in January 1974. Comparatively low values, i.e. less than 2×10^5 cells l^{-1}, were observed at irregular intervals throughout the study. A similar pattern of seasonal change took place in terms of cell volume with, for example, a maximum standing crop of about 7.5×10^7 μm^3 l^{-1}

Table 8a. List of algae floating in Highland Water which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Achnanthes minutissima v. *cryptocephala*
Achnanthes saxonica
Cocconeis placentula v. *euglypta*
Fragilaria capucina v. *lanceolata*
Navicula gregaria
Nitzschia dissipata
Nitzschia palea
Rhoicosphenia curvata
Synedra ulna v. *danica*
Scenedesmus quadricauda
Chlamydomonas sp.
Aphanothece sp.

Table 8b. List of planktonic algae collected from Highland Water which accounted for between 1 and 10% of the flora on at least one sampling date.

Stephanodiscus hantzschii
Chlamydomonas monadina
Scenedesmus dimorphus
Scenedesmus quadricauda v. *parva*

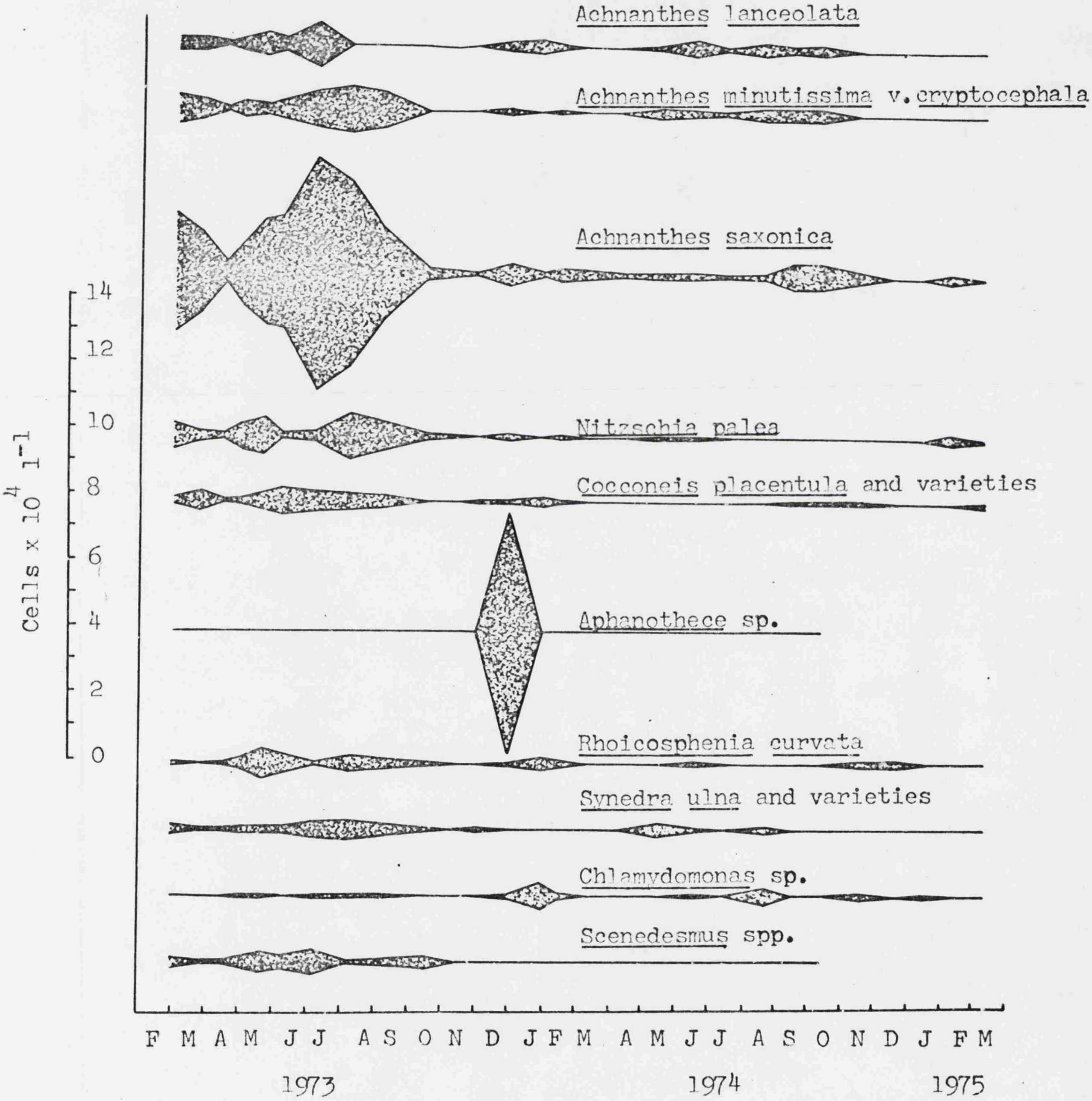

Fig. 17. Seasonal changes in the standing crop of common algae floating in Highland Water.

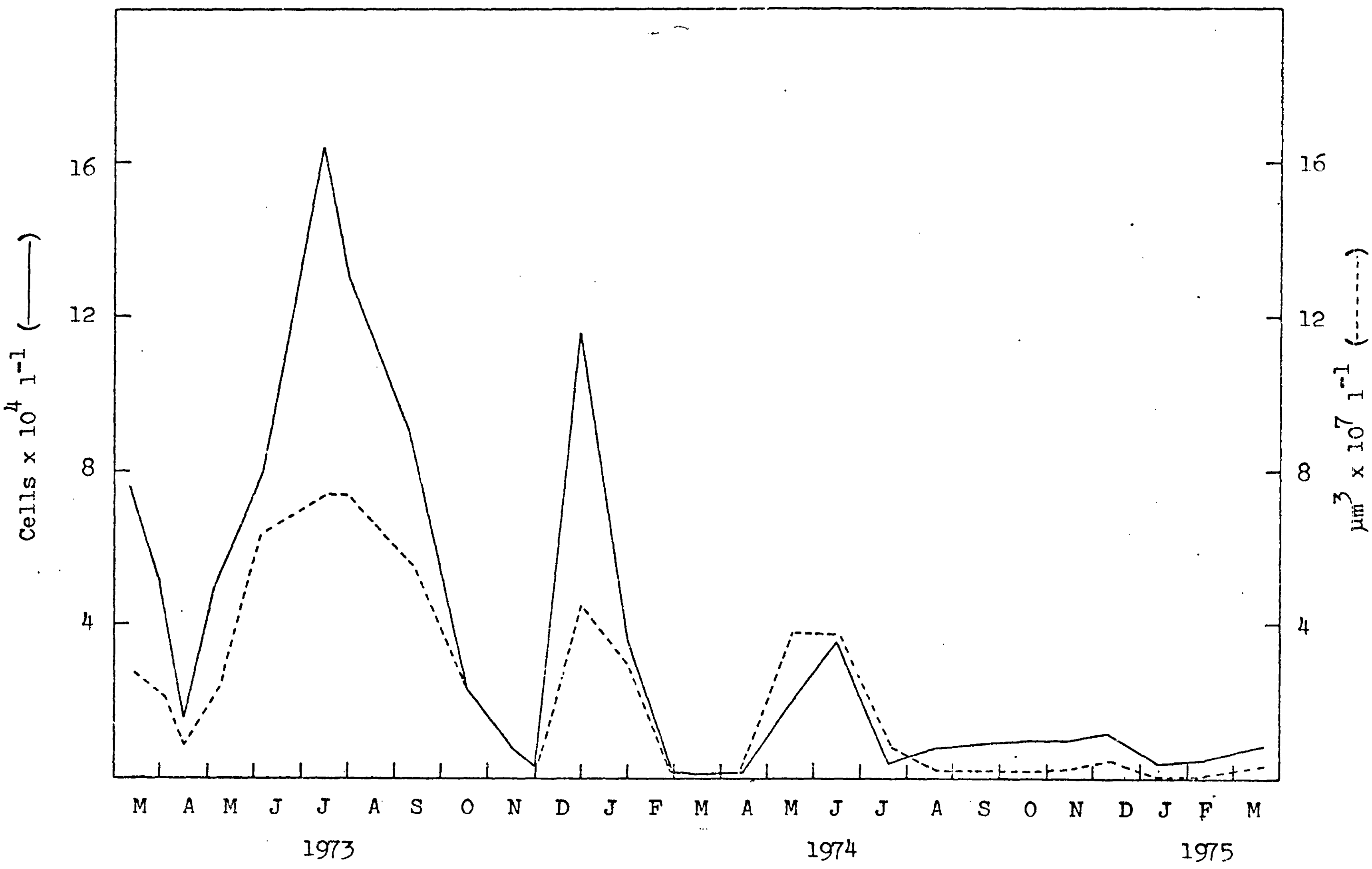

Fig. 18. Seasonal changes in the standing crop of the entire algal assemblage floating in Highland Water.

being recorded during the summer of 1973.

The fastest daily rate of recruitment into the plankton in terms of numbers, 3.8×10^3 cells l^{-1}, occurred during December 1973 (Fig. 18), mostly due to the appearance of Aphanothece (Fig. 17), but high values, i.e. $1.5 - 1.7 \times 10^3$ cells l^{-1}, were also observed during April and June 1974. In terms of volume, the fastest daily recruitment rate, 1.4×10^6 μm^3 l^{-1}, again occurred in December 1973, but comparable values, i.e. $1.1 - 1.3 \times 10^6$ μm^3 l^{-1}, were also observed during the late spring of both years.

Epiphytic Communities

Large quantities of decaying tree branches occurred in Highland Water and provided the only substrate for epiphytic algae in the area. Usually the diatom Achnanthes saxonica maintained dominance in this habitat accounting for 40 - 63% by numbers of the total algal flora. It was followed in order of descending importance by Achnanthes minutissima v. cryptocephala, Gomphonema parvulum and other forms that were typically found on the rocks of the stream. However, at least 20% of the flora was more characteristic of the assemblage observed on the sediments, a point illustrated by the continual presence of Navicula spp. (especially N. cryptocephala), Nitzschia linearis, Fragilaria capucina v. lanceolata and Synedra ulna. Several other forms, notably Surirella ovata v. minuta, achieved considerable importance (5 - 10% by numbers) in this habitat but nowhere else. Due to the difficulty in removing all the algae from the wood, estimates of standing crop were not made.

Discussion

Since the epipelic communities in Highland Water began to expand significantly in May of both years, they contrast with those from the Avon River in which the corresponding period of development occurred in March. This time lag is almost certainly due to the fact that the amount of light reaching the surface of the stream was, through the shading effect of the trees, relatively lower than in the Avon. As in the Avon during the summer of 1974 when no severe flooding took place, the population from Highland Water decreased continuously during the warmer months of both years. Since water levels remained relatively constant at these times the quality of the sediments may, as in the Avon, have deteriorated during the period of high standing crop. One noticeable difference between the samples from the two years is that, with the exception of *Pinnularia biceps* and *P. biceps* f. *petersenii*, all of the common species occurred much less abundantly in 1974 than in 1973 despite the fact that there was no conspicuous shift in environmental conditions. Although the abundance of most species fell in 1974, little change occurred in the standing crop of the total assemblage due to the increase in numbers of the relatively large *P. biceps*.

The fact that the density of epilithic algae in Highland Water did not show a very marked change throughout the year is surprising considering the great fluctuations in light and temperature. This feature is clearly related to the pattern of growth of the predominant species, *Achnanthes saxonica*, an alga exhibiting no characteristic increase in growth during the spring and showing no marked decline during the winter. That two significant blooms, made up almost entirely of *Gomphonema* and *Synedra* spp., occurred at all four sites during the spring and early summer, more or less coincident with similar upsurges in the epipelic community, suggests that, as in the Avon, the quantity of light was regulating the rate of growth of these species.

The density of *Achnanthes saxonica* remained almost unchanged throughout the year at Sites I and II, where the water velocity was high, but fluctuated a great deal in the slower flowing areas, indicating that this species is apparently best adapted to conditions where there is a rapid flow of water, as is also the case with several other epilithic forms (Dillard, 1971). The constancy of the density of A. saxonica at Sites I and II during the severe flooding in part of 1974 contrasts with the considerable fall in standing crop in areas III and IV. This indicates that representatives of this species living in rapid water are more securely attached to the substrate than those inhabiting slower reaches and are thus better able to withstand increases in discharge.

Although Blum (1954) and Müller-Haeckel (1966) demonstrated a diurnal rhythm in the numbers of Nitzschia palea present in stream potamoplankton, a feature related to photosynthetic activity and detachment, this was not a universal feature of the entire community. The plankton samples in the present study were always taken at the same time of day in order to standardize this source of variation. As changes in the standing crop of the flora of Highland Water during most of 1973 paralleled those exhibited by the epipelic assemblage, detachment from the sediments seems to be a major source of variation in algal density within the potamoplankton, a view further substantiated by the fact that many of the species were common to both assemblages. In contrast to both the epipelic and epilithic communities, however, a sharp increase in numbers took place during January 1974. Since this shift was not correlated with a decrease in water volume or an increase in scouring, it appears that a mid winter upsurge in the algal community occurred upstream from the study area. This view is further supported by the fact that the predominant form in the potamoplankton, Aphanothece sp., was relatively scarce in the attached assemblages. During March 1974, the density of the algae fell to unusually low levels, a feature correlated with exceptionally high discharge rates. Expressing the data of this month in terms of more typical flow conditions, i.e. 50 l sec^{-1}, however, gives a relatively high value of about 9×10^4 cells l^{-1}, presumably reflecting the effect of scouring on algal attachment. The sharp increase in the density of the algae during May and June 1974 and their subsequent fall, parallels again the changes recurring in the epipelic community.

The community of algae attached to the decaying tree branches in Highland Water differed considerably from those growing on living plants (Chudyba, 1965, 1968; Whitton, 1970) and on decaying tree stumps (Whitford and Schumacher, 1963; Clafin, 1968). However, at least two of the more common species, Achnanthes minutissima v. cryptocephala and Gomphonema parvulum, seem to be typical epiphytic forms (e.g. Round, 1957b; Whitton, 1970). Since Achnanthes saxonica was predominant on both the branches and rocks, there was presumably a considerable degree of similarity in the properties of the substrate surface.

One of the striking features of this investigation is the relatively low standing crop of the algal flora throughout the stream. Since nitrates, phosphates and silicates always occurred in relatively large amounts, these densities reflect, at least in part, the low alkalinity levels which, in other studies, have been shown to be inhibitory (Shane et al., 1971; Dickman, 1973). As only a small quantity of light penetrated through the canopy of branches and leaves, this may also have limited development. For example, algae cultured in the laboratory (mainly Melosira varians, Achnanthes minutissima v. cryptocephala and Diatoma vulgare) at 15°C on smooth rocks at a light intensity comparable to that reaching the surface of Highland Water developed at only 1 - 2% of the rate exhibited by a similar community in unshaded conditions. Large numbers of larval lampreys occurred in the stream but their gut contents consisted almost entirely of detritus (see page 104) as was also the case with the invertebrate fauna.

River Wylye

Samples of algae were collected from a site on the River Wylye (Lat. 51° 09' ; Long. 2° 11') and also from an area on a small tributary immediately downstream. The Wylye, measuring about 50 km in length and falling 130 m to its juncture with the River Nadder, is about 20 m in width in the vicinity of the collection area. Epipelic algae and samples of epiphytes growing on water cress were sampled from an unshaded site along the bank while epilithic forms were collected from mid-stream. The tributary of the Wylye, measuring approximately one km in length and three m in width, supports an extensive growth of water cress near its source. Immediately downstream from this area, however, the water passes through a short concrete sluice-way into a stream about 120 m in length which discharges into the Wylye. Epilithic algae and epiphytes associated with Cladophora glomerata were collected in the sluice from stones measuring 5 - 15 cm in diameter, while the epipelic flora was sampled from a downstream area near the bank. Samples of episammic algae were taken from mid stream and the potamoplankton and true plankton from just before the point where the tributary entered the main river.

Physico-chemical Analyses

Water temperatures in the River Wylye increased from $10^{\circ}C$ in March to $15.5^{\circ}C$ in June but then fell inconsistently to $4.5^{\circ}C$ by November (Fig. 19). Thereafter, a gradual increase occurred until a value of $16.5^{\circ}C$ was attained near the end of August. During the following winter, temperatures remained relatively high, seldom falling below $9^{\circ}C$. Discharge fell erratically from 0.5 - 0.23 m^3 sec^{-1} between March and December 1973 but then exhibited a very marked increase to 0.8 m^3 sec^{-1} during the early part of 1974 (Fig. 20). Values subsequently declined, reaching 0.28 m^3 sec^{-1} in August but increased to over 0.70 m^3 sec^{-1} by December. The rate of water flow over the epipelic and epiphytic collection sites ranged from 4 - 15 cm sec^{-1} during 1973 but rose to 28 cm sec^{-1} during the floods in the early part of 1974 (Fig. 19). Values subsequently decreased gradually, falling to 2 cm sec^{-1} by August, but during December rose to 22.5 cm sec^{-1}. Water depth at this collection site varied

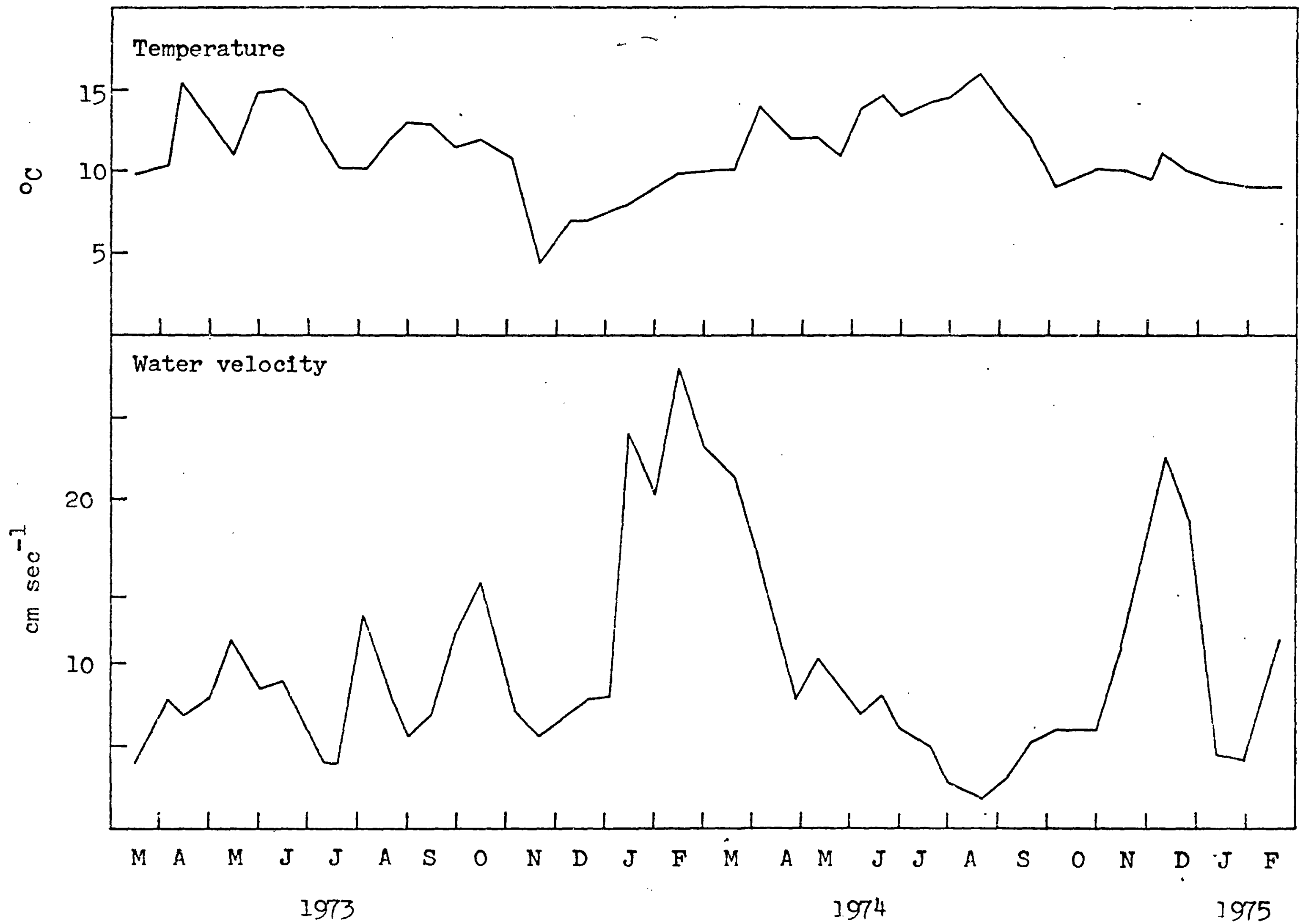

Fig. 19. Seasonal changes in the temperature of the River Wylye together with the water velocity over the epipelic collection sites.

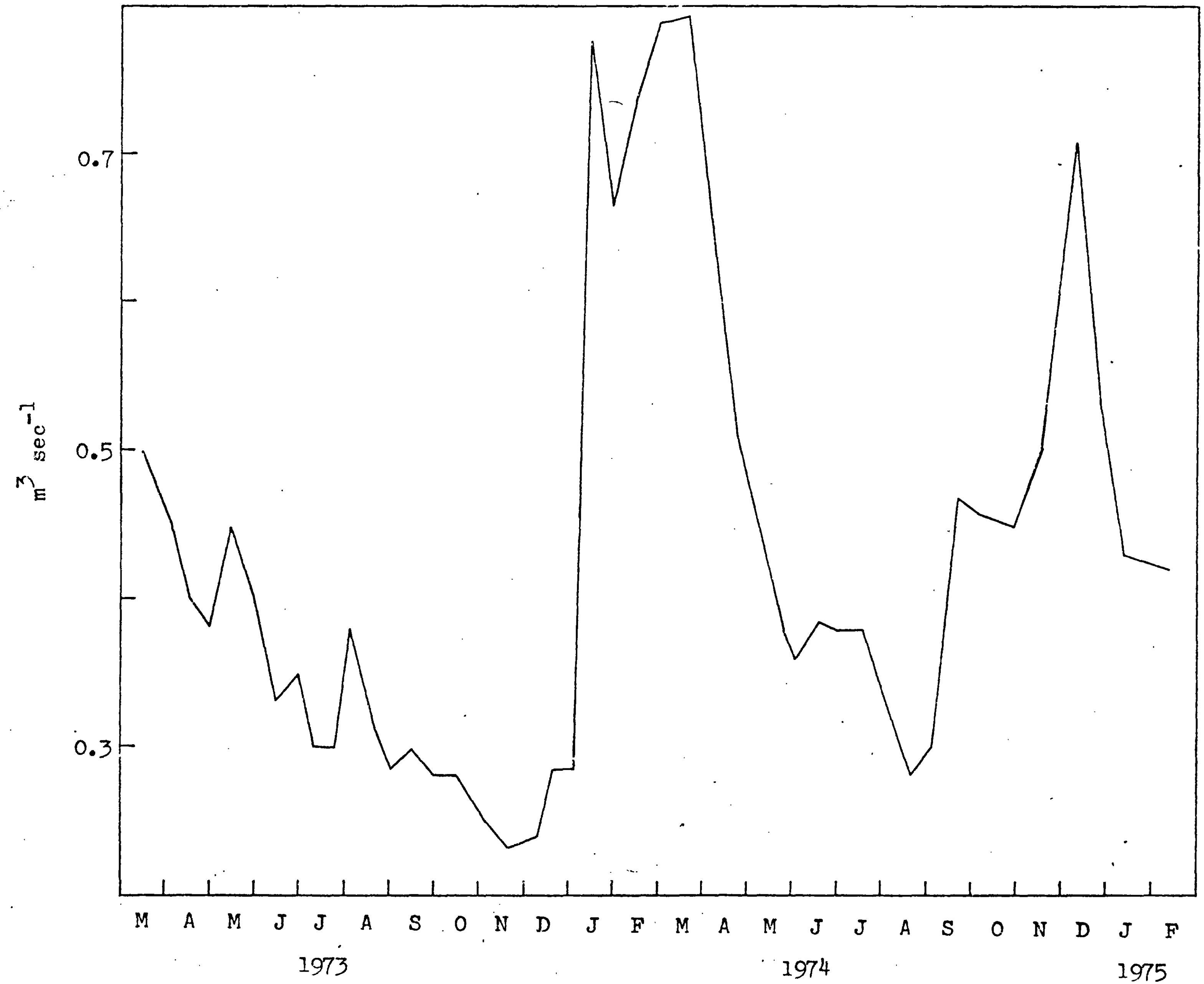

Fig. 20. Seasonal changes in the discharge rate of the River Wylye.

from 10 – 25 cm. The rate of water flow over the epilithic collection area varied from 35 – 60 cm sec^{-1}, and the depth fluctuated from 30 – 45 cm. The pH of the river remained comparatively high, i.e. 7.4 – 8.1 , and nutrients always occurred abundantly (Table 9). The organic content of the sediments averaged about 16% of the total dry weight with maximum and minimum values of 21.5 and 12% respectively.

Seasonal changes in the temperature of the tributary bore great similarity to those outlined above. During the winter, however, the temperature fell to about 3°C while in the summer values of up to 17.5°C were recorded. Discharge was relatively constant, averaging 0.04 m^3 sec^{-1} ,with maximum and minimum values of 0.06 and 0.025 m^3 sec^{-1} , while the mean water velocity over the epilithic, epipelic and episammic collection sites was approximately 35, 8 and 25 cm sec^{-1} respectively. The water depth at the three sites also did not vary greatly, the respective mean values being 11, 5 and 20 cm. The pH and nutrient content of the water was similar to that exhibited by the Wylye and the organic content of the sediments averaged 20% with a range of 16 – 28%.

Epipelic Communities

The epipelic community in the River Wylye was extremely diverse, comprising a total of 278 different species, varieties and forms of algae. The Bacillariophyta predominated with 242 taxa, followed by the Chlorophyta with 15, the Cyanophyta with 14, the Euglenophyta with five and the Chrysophyta with two. The most common members of the first group of algae were <u>Achnanthes lanceolata</u>, <u>A. minutissima</u> v. <u>cryptocephala</u>, <u>Melosira varians</u>, <u>Nitzschia linearis</u> and <u>N. palea</u> and varieties (Table 10 , Fig. 21), while the <u>Chlorophyta</u> were represented mainly by <u>Chlamydomonas monadina</u>, <u>Closterium acerosum</u> and <u>C. lunula</u>. <u>Oscillatoria limosa</u> and <u>O. brevis</u> were the most abundant of the Cyanophyta while the Euglenophyta were represented by the occasional specimen of <u>Euglena</u> sp.

Only a few algal species in the epipelic assemblage exhibited very well defined and similarly recurring patterns of succession. <u>Opephora martyi</u>, the best example, attained peak abundance towards the end of May in both years when it reached densities of 3.4 x 10^5 and 3.1 x 10^5 cells cm^{-2} respectively. Although <u>Nitzschia linearis</u>

Table 9. Physico-chemical properties of water from the River Wylye during 1973 and 1974. Except for pH, all data are expressed in terms of mg l^{-1}.

Parameter	Average	Range
pH	7.9	7.4 - 8.1
Total Alkalinity	190	110 - 240
Silica	6.5	2.0 - 2.6
Orthophosphate-Phosphorus	0.7	0.2 - 2.6
Nitrate-Nitrogen	3.7	1.5 - 5.2

Table 10. List of epipelic algae collected from the River Wylye which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Achnanthes minutissima v. *cryptocephala*
Cocconeis placentula v. *euglypta*
Cyclotella comta
Fragilaria capucina v. *lanceolata*
Fragilaria construens
Fragilaria intermedia
Fragilaria leptostauron
Melosira varians
Meridion circulare
Nitzschia dissipata
Nitzschia linearis
Nitzschia palea
Nitzschia palea v. *debilis*
Opephora martyi
Surirella ovata v. *minuta*
Synedra acus
Synedra ulna
Oscillatoria limosa

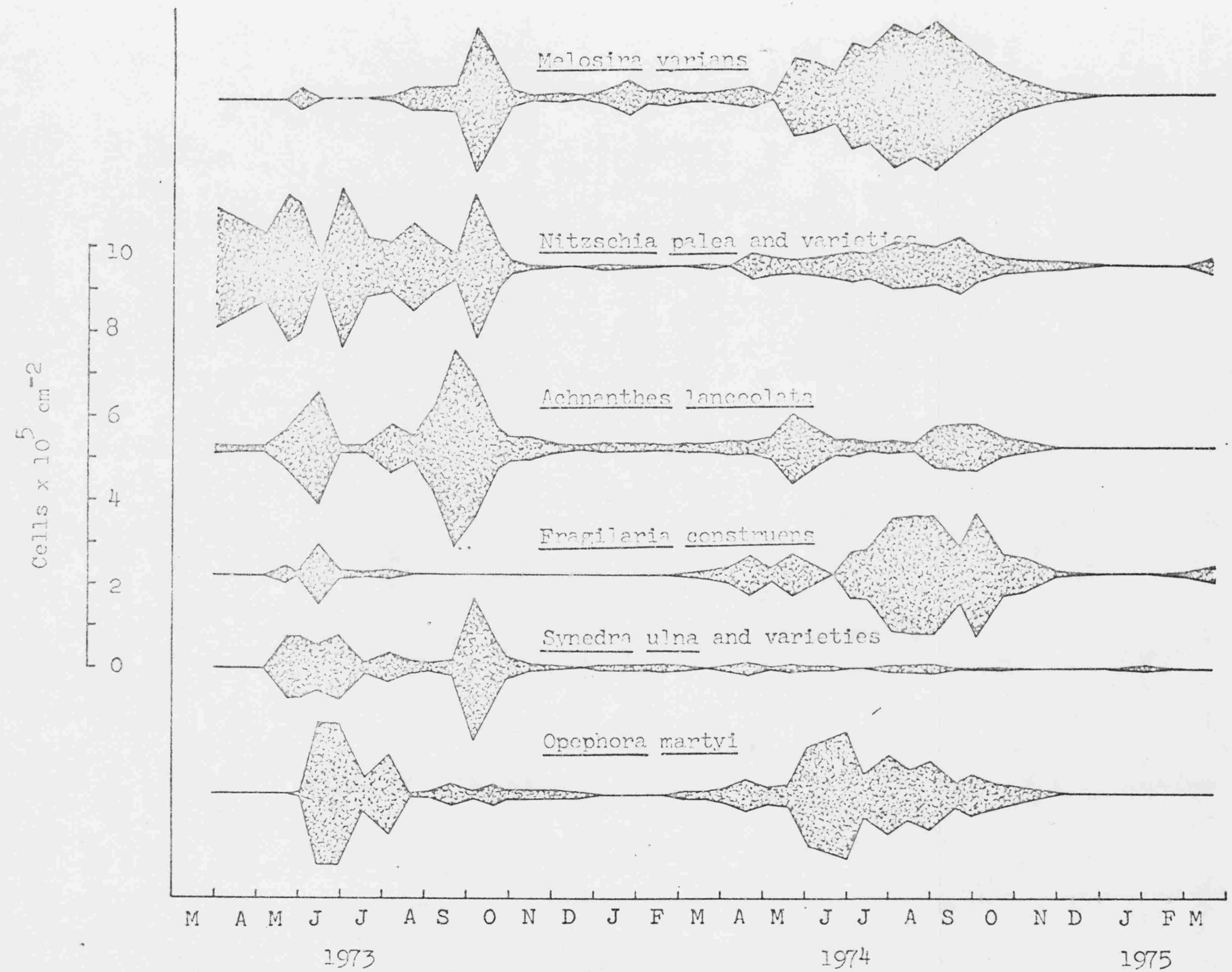

Fig. 21. Seasonal changes in the standing crop of common epipelic algae in the River Wylye.

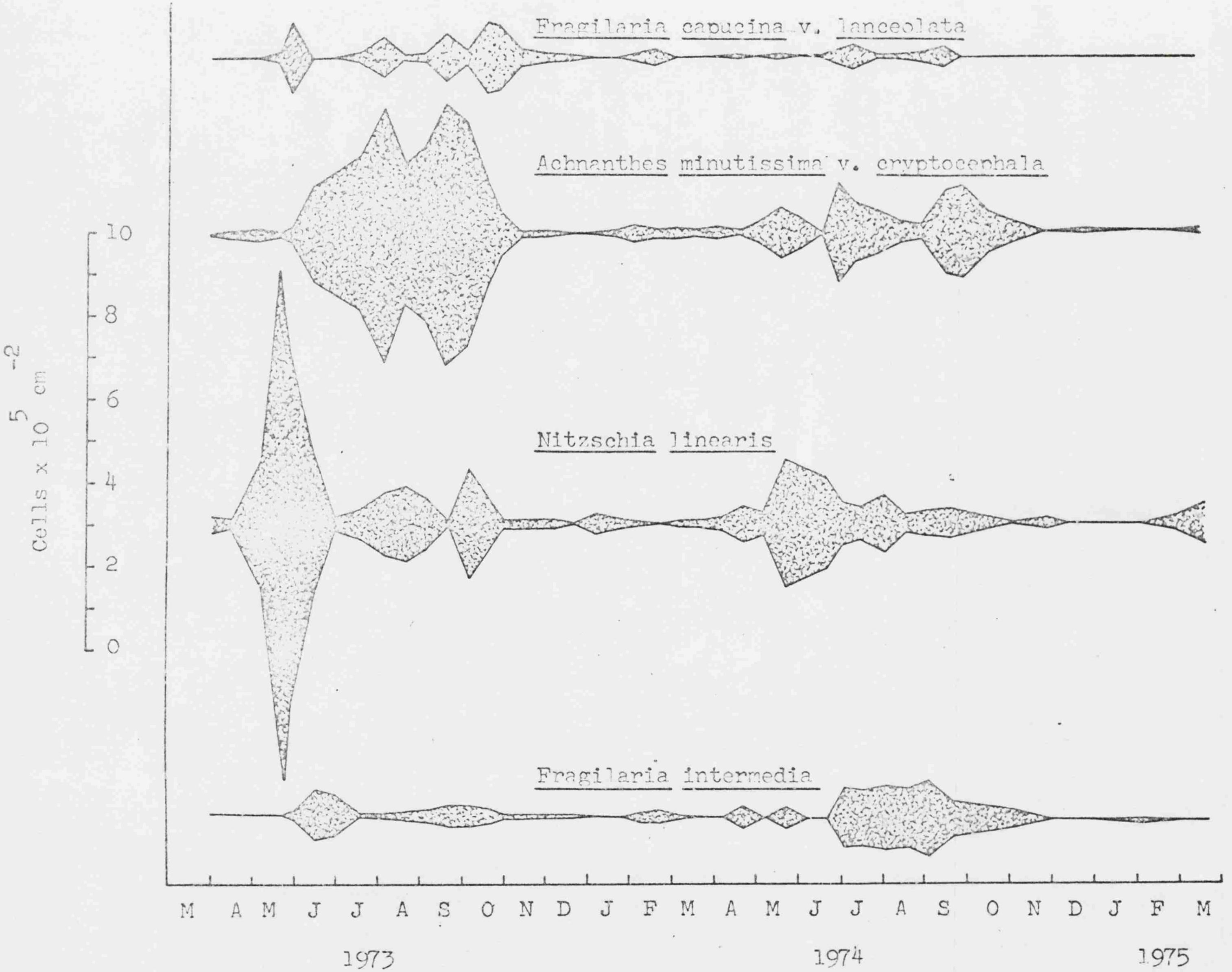

Fig. 21 (Cont'd.). Seasonal changes in the standing crop of common epipelic algae in the River Wylye.

reached its greatest abundance during the middle of April in both years, considerable variation existed in the standing crop of the species at this time, i.e. 1.2×10^6 cells cm^{-2} in 1973 and 3.0×10^5 cells cm^{-2} in 1974. Precisely the same sort of pattern was exhibited by Achnanthes lanceolata, A. minutissima v. cryptocephala and Nitzschia palea. On the other hand, several other species , e.g. Fragilaria construens, F. intermedia and Melosira varians, occurred much more abundantly in 1974 than in 1973 and considerable variation existed in the periods of greatest **density.**

Significant development of the entire assemblage began during April and May of 1973 with numbers rising from 0.7×10^6 to 3.4×10^6 cells cm^{-2} (Fig. 22). Numbers fluctuated during the summer but exhibited another pronounced peak early in September. A sharp fall in algal numbers took place immediately after this latter month and comparatively low levels were maintained throughout the winter. The spring bloom during 1974 began in March and relatively little variation, i.e. $1.2 - 1.8 \times 10^6$ cells cm^{-2}, existed in the standing crop of the flora during the whole of the following summer. In terms of cell volume virtually the same pattern of change occurred in 1973 as that outlined for numbers. However, in 1974, a gradual, but inconsistent decrease in standing crop was observed from April onwards.

Although the fastest daily growth rate of the epipelic flora in 1973, 1.1×10^5 cells cm^{-2} , took place during the spring bloom, a nearly comparable value, 1.0×10^5 cells cm^{-2}, was recorded in August (Fig. 22). During 1974, however, the fastest daily rates, i.e. 0.6 $\times 10^5$ and 0.55×10^5 cells cm^{-2}, occurred in June and April respectively. In terms of cell volume, the fastest daily rates, 2.5×10^8 μm^3 cm^{-2}, were observed during April, August and September 1973 while, in 1974, maximum values of only 0.95×10^8 (April) and 0.5×10^8 (June) μm^3 cm^{-2} were recorded. Algae disappeared from the sediments most quickly during September and June 1973 when values of 1.25×10^5 cells cm^{-2} (2.45×10^8 μm^3 cm^{-2}) were recorded. In 1974, much lower disappearance rates, i.e. 0.3×10^5 cells cm^{-2} (September) and 0.7×10^8 μm^3 cm^{-2} (June), occurred.

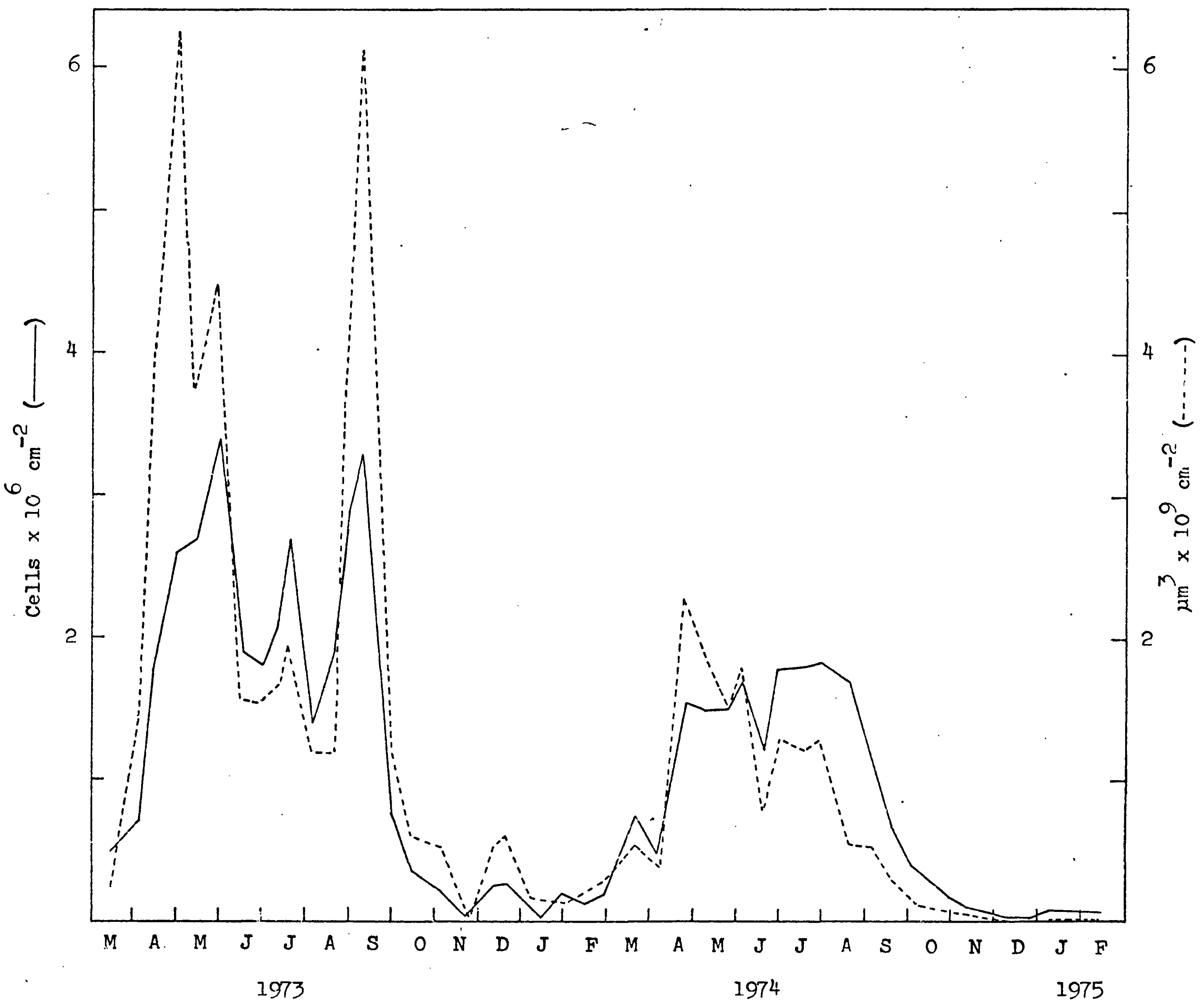

Fig. 22. Seasonal changes in the standing crop of the entire epipelic assemblage in the River Wylye.

The epipelic community in the tributary remained less diverse than that of the main Wylye possessing 192 different species, varieties and forms. Diatoms once again predominated with 148 taxa, the most common species being identical to those found in the Wylye. Members of the Chlorophyta were second in importance with 13 species followed by the Cyanophyta with 12 and the Euglenophyta with three. The predominant species in these last three groups were generally similar to those described for the main Wylye.

Many of the patterns exhibited in terms of peak abundance by the epipelic flora were less prominent in the tributary than in the Wylye, with good examples being provided by Opephora martyi, Melosira varians and Nitzschia palea (Fig. 23). Several other species on the other hand, e.g. Synedra ulna, Achnanthes minutissima v. cryptocephala, Fragilaria capucina v. lanceolata, exhibited seasonal patterns of abundance that virtually paralleled those already described for these taxa in the main river.

The density of the entire community increased sharply during April 1973 from 1.8×10^6 to 8.1×10^6 cells cm^{-2} (Fig. 24), the numbers subsequently fluctuating a great deal thus paralleling the situation in the main Wylye. A considerable fall in numbers occurred during September and it was not until the beginning of April 1974 that a significant recovery was apparent, at which time the density reached 2.9×10^6 cells cm^{-2}. The pattern of change during the remainder of 1974 was characterised by a gradual fall in numbers. Changes in the standing crop in terms of cell volume during both 1973 and 1974 roughly paralleled those outlined for numbers with a maximum density of 14.1×10^9 μm^3 cm^{-2} in the former year and 5.0×10^9 μm^3 cm^{-2} in 1974.

The fastest daily rate of expansion of the epipelic community in the tributary exceeded that observed in the main Wylye (Fig. 24). For example, during 1973 the highest rate in terms of numbers was 3.1×10^5 cells cm^{-2} (April) while by volume the greatest value was 6.6×10^8 μm^3 cm^{-2} (August). Similarly, during 1974 maximum daily rates of 1.4×10^5 cells cm^{-2} (April) and 1.5×10^8 μm^3 cm^{-2} (March) were recorded. Algae disappeared rapidly from the sediments in the summer of 1973 at a time when, through the artificial control

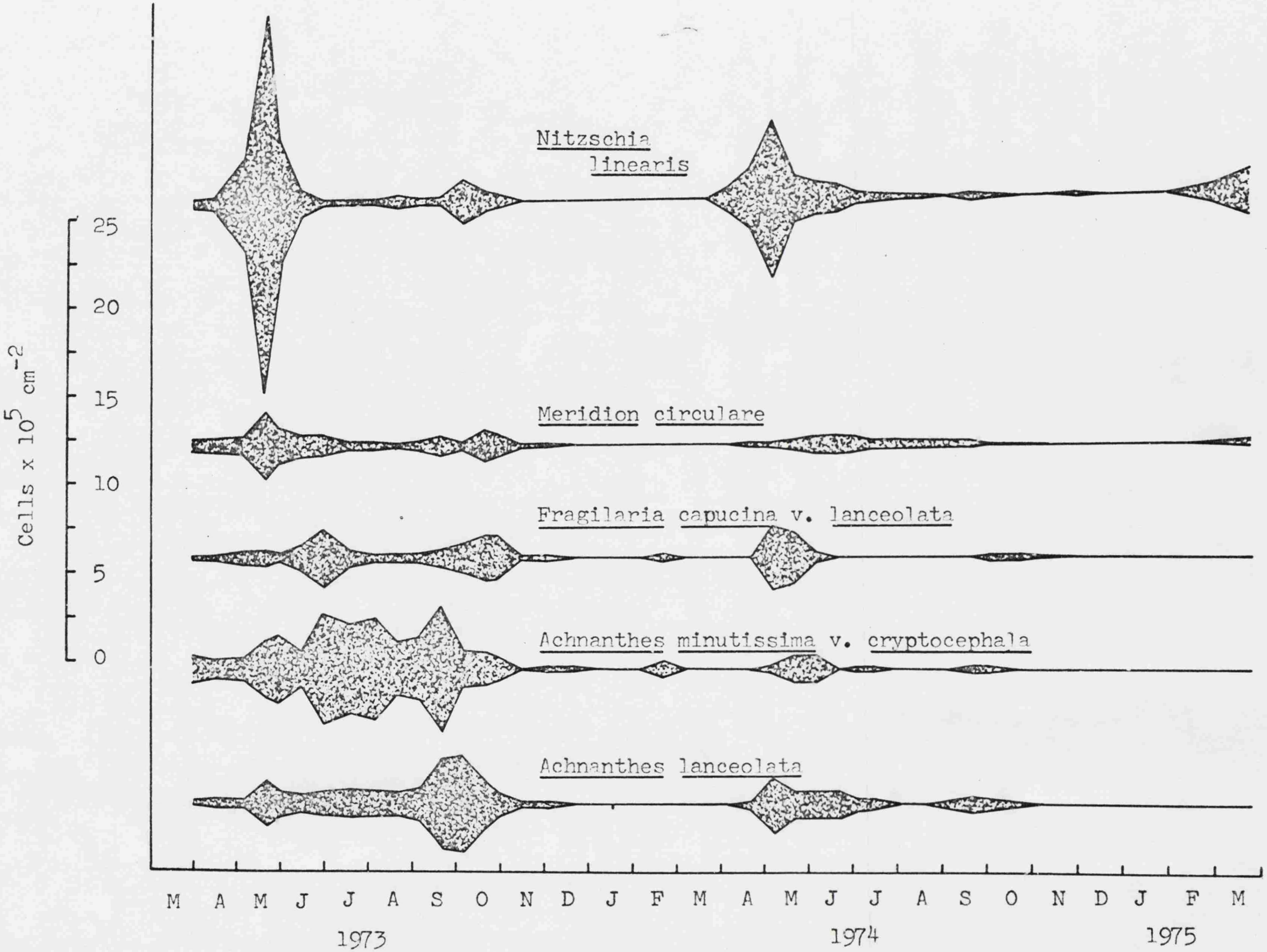

Fig. 23. Seasonal changes in the standing crop of common epipelic algae in the tributary of the River Wylye.

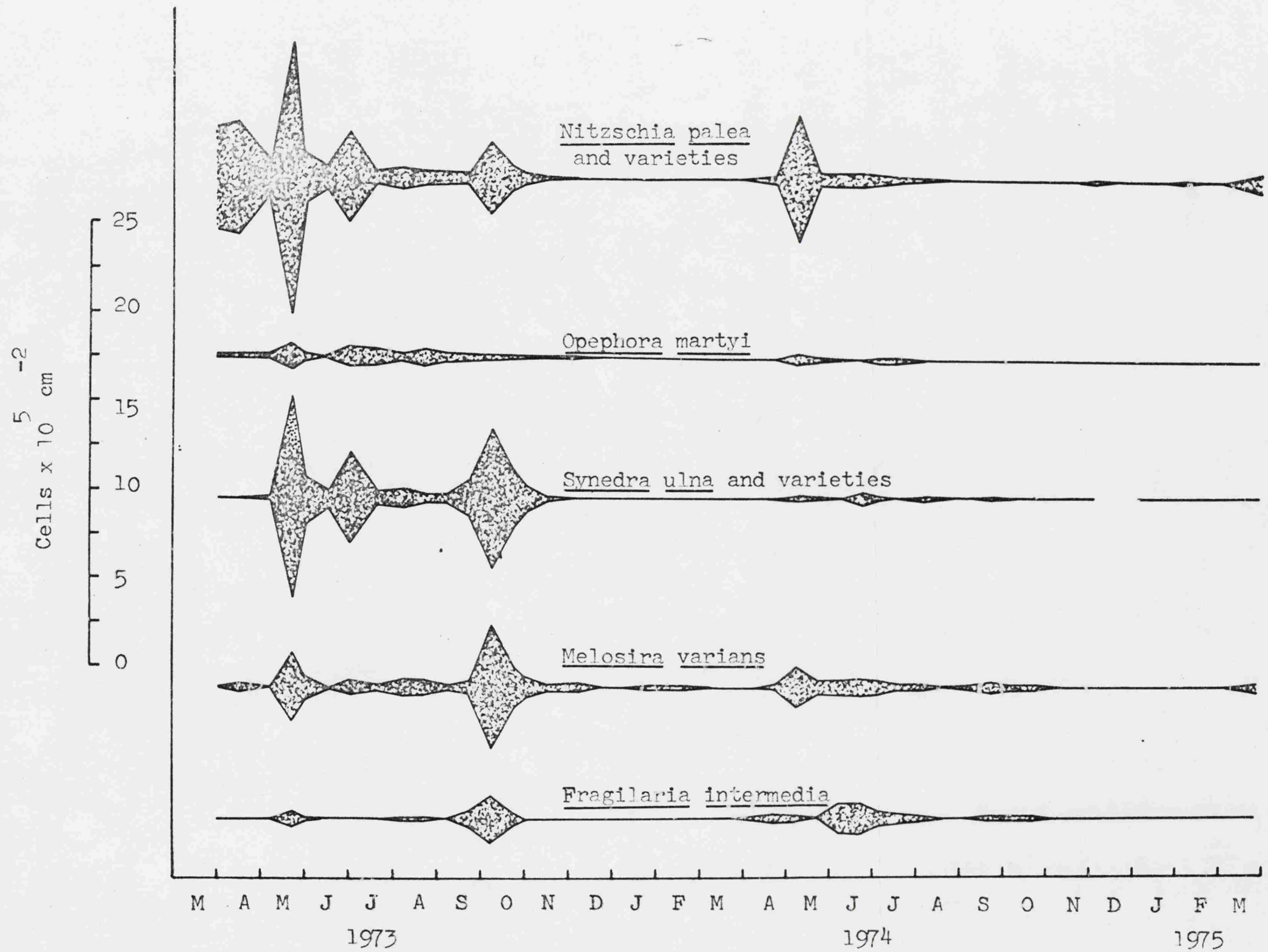

Fig. 23 (Cont'd). Seasonal changes in the standing crop of common epipelic algae in the tributary of the River Wylye.

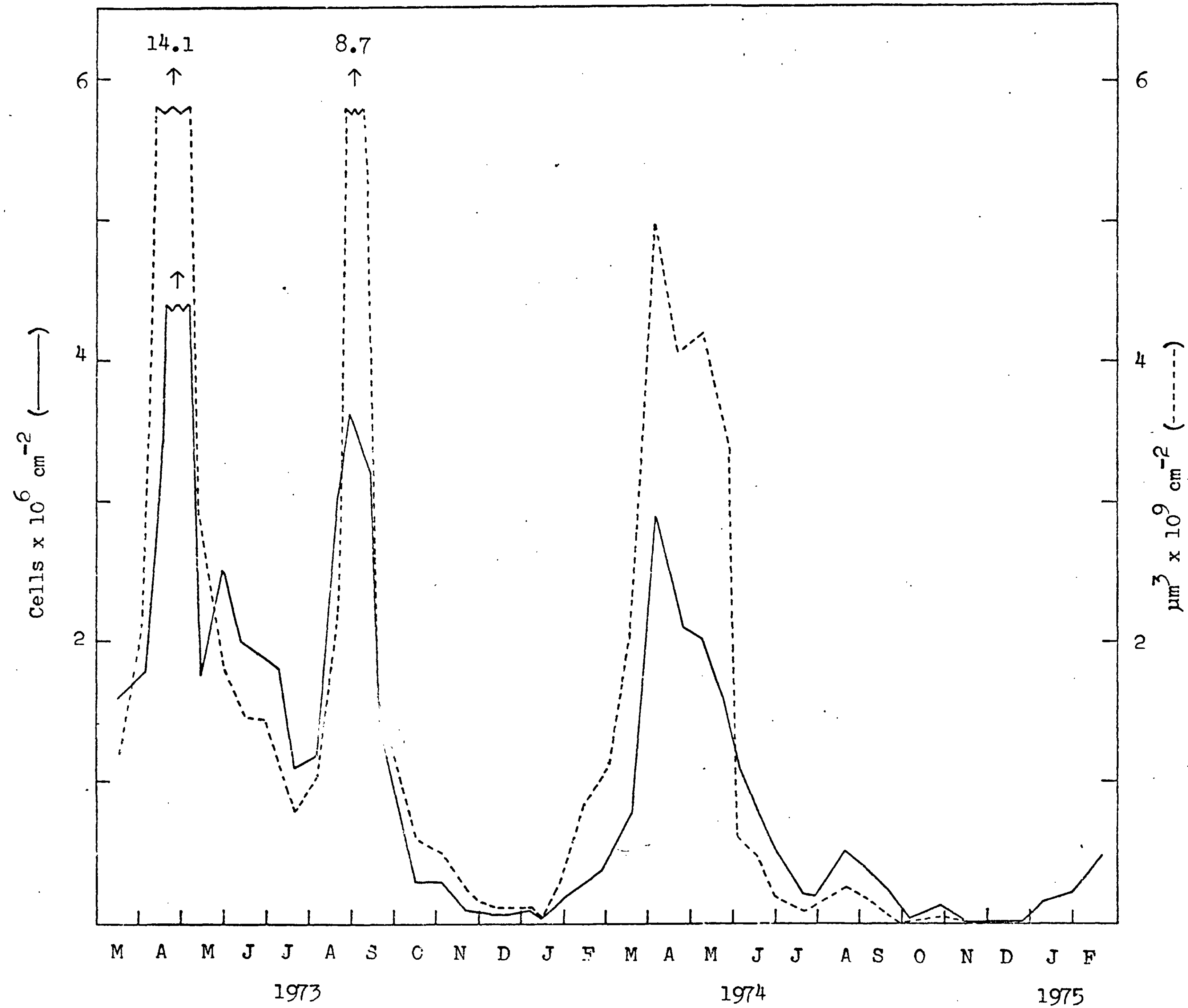

Fig. 24. Seasonal changes in the standing crop of the entire epipelic assemblage in the tributary of the River Wylye.

of discharge rates, there was no severe flooding. Maximum daily values of 3.0×10^5 cells cm^{-2} (May) and 1.8×10^5 cells cm^{-2} (September) were recorded but, in 1974, the highest value was only 0.4×10^5 cells cm^{-2}.

Episammic Community

The episammic community in the tributary was highly restricted with only 13 taxa being found. Diatoms accounted for 12 species, the remaining taxon belonging to the Cyanophyta. The most common species, Amphora ovalis v. pediculus, occurred abundantly, i.e. up to 4.7×10^5 cells cm^{-2}, between June and September 1973 but during the summer of 1974 was comparatively restricted, a pattern virtually opposite to that exhibited by Opephora martyi (Fig. 25). Although a difference of 1½ months existed in the phasing of the seasonal peaks, the abundance of Fragilaria construens was similar in both years.

The total standing crop of the episammic community did not exhibit a spring bloom in 1973, but did increase from 0.2×10^5 cells cm^{-2} in March to 6.0×10^5 cells cm^{-2} in early September (Fig. 26). The standing crop subsequently decreased sharply to a density of only 1×10^2 cells cm^{-2} in January. A well defined spring bloom did, however, occur in March of 1974 with values subsequently rising to 5.2×10^5 cells cm^{-2} in May only to fall gradually again to less than 1×10^3 cells cm^{-2} in the winter. As with numbers, the maximum standing crops in terms of volume were also observed in September 1973 and May 1974 (Fig. 26). The fastest daily growth rate recorded during the study, 1.7×10^4 cells cm^{-2}, took place during September 1973 while in 1974 the most rapid rate, 0.7×10^4 cells cm^{-2}, was observed during the spring bloom. In terms of cell volume, the highest daily rate, 7.0×10^6 μm^3 cm^{-2}, was recorded in July 1973 with the second fastest rates, 4.5×10^6 μm^3 cm^{-2} occurring during September and May of 1973 and 1974 respectively. The episammic algae disappeared from the sand at the relatively fast daily rate of 2.1×10^4 cells cm^{-2} during October 1973 but at other times, such as in June 1974, lower values, e.g. 2.0×10^4 cells cm^{-2}, were recorded.

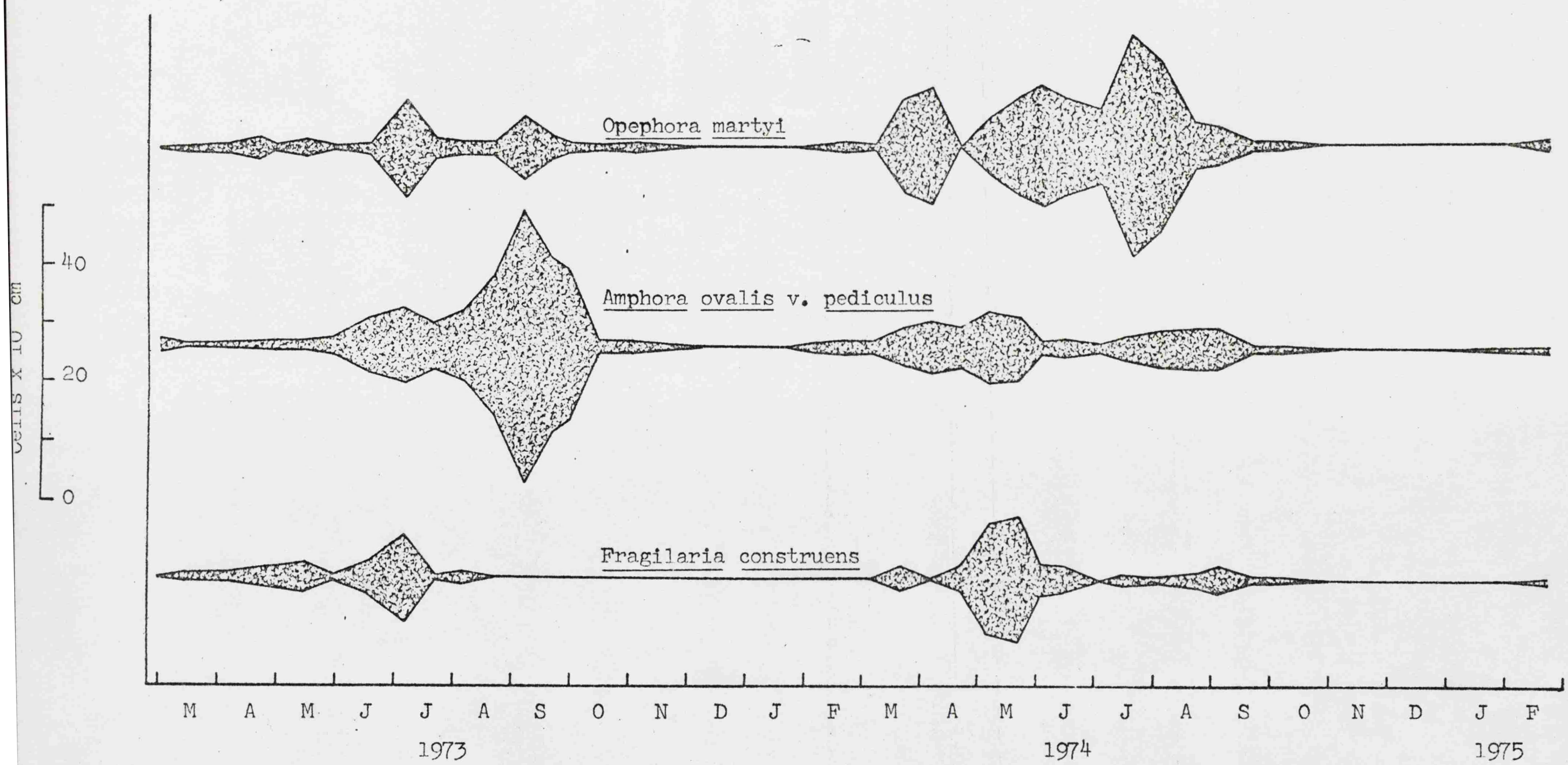

Fig. 25. Seasonal changes in the standing crop of common episammic algae in the tributary of the River Wylye.

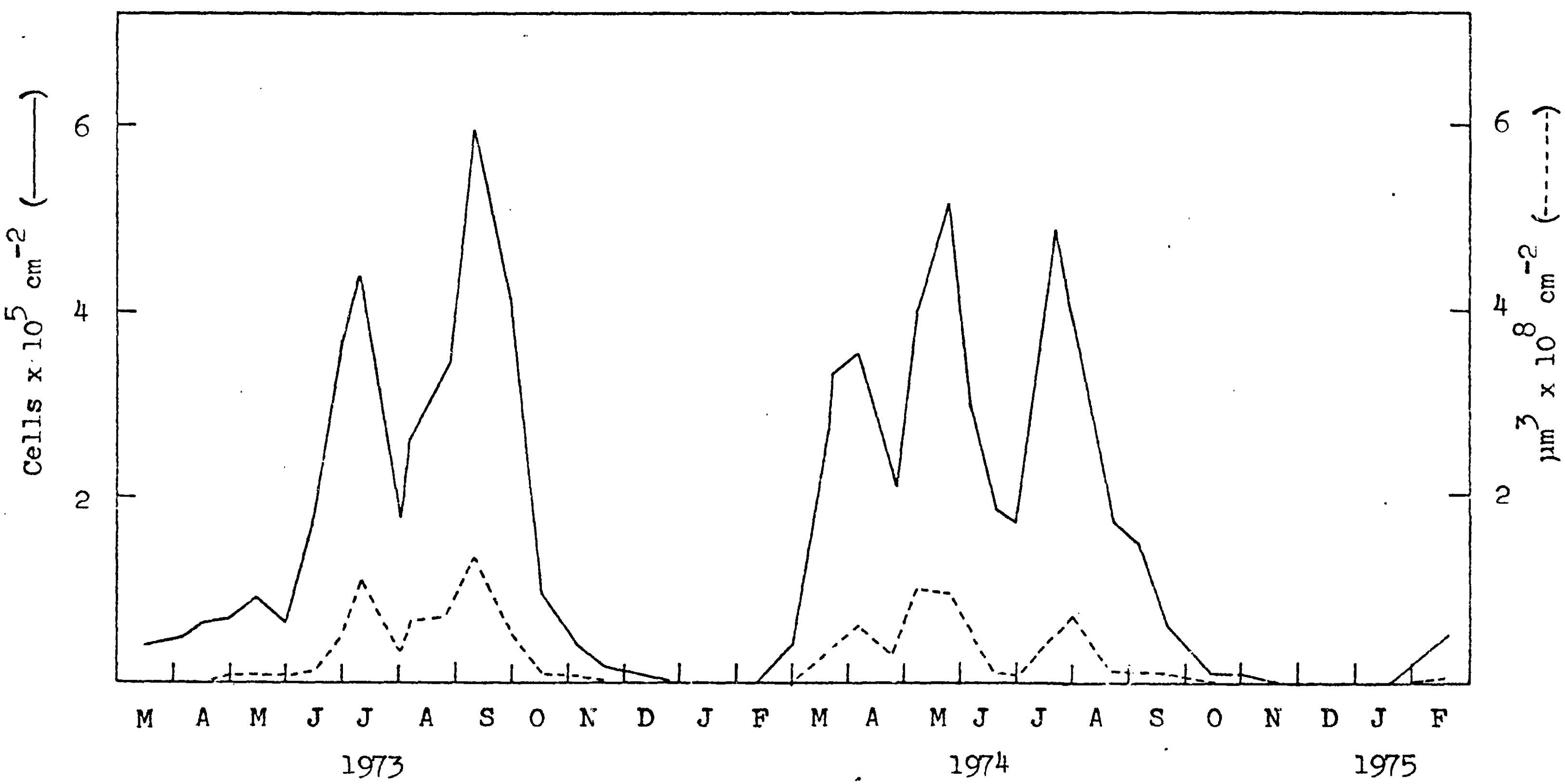

Fig. 26. Seasonal changes in the standing crop of the entire episammic assemblage in the tributary of the River Wylye.

Epilithic Communities

The epilithic assemblage collected from the River Wylye was highly restricted with only 91 different kinds of algae occurring on the rocks (Table 11). There were 86 different species and varieties of the Bacillariophyta and five of the Cyanophyta. Amphora ovalis v. pediculus was by far the most common algae on the rocks from March 1973 until January 1974 when it always accounted for at least 60% of the total flora. Immediately after the severe winter floods in March, however, the abundance of this species fell sharply with Opephora martyi, Cocconeis placentula v. euglypta, Nitzschia palea and Melosira varians rising in importance. During the following summer, Phormidium foveolarum attained dominance (60 - 90%) but was subsequently replaced by Amphora ovalis v. pediculus. Throughout the investigation, Achnanthes minutissima v. cryptocephala accounted for 10 - 25% of the algal flora.

The standing crop of the entire assemblage remained relatively constant ($0.7 - 1.4 \times 10^6$ cells cm^{-2}) from the beginning of the study in March 1973 until November, but subsequently waned to 0.2×10^5 cells cm^{-2} by February 1974 (Fig. 27). Thereafter, a sharp increase took place but it was not until June that a further sustained rate of increase in density occurred. The standing crop subsequently decreased sharply to $0.5 - 1.5 \times 10^5$ cells cm^{-2}, a level maintained until February 1975. In terms of cell volume, the amount of algae on the rocks averaged $0.07 - 0.2 \times 10^9$ μm^3 cm^{-2} during most of 1973 but thereafter fell to insignificant levels. A small increase in abundance occurred during March but peak values, 2.0×10^9 μm^3 cm^{-2}, were not recorded until July. Thereafter, the standing crop fell to only 1.0×10^7 μm^3 cm^{-2}. The daily growth rate of the algae was always relatively slow with maximum values of 0.8×10^5 cells cm^{-2} (1.0×10^8 μm^3 cm^{-2}) and 0.3×10^5 cells cm^{-2} (0.3×10^8 μm^3 cm^{-2}) occurring during June and July of 1974 respectively. The fastest daily rates of disappearance from the rocks, 4.4×10^4 cells cm^{-2}, took place during July and August 1974.

The epilithic community in the tributary remained comparatively diverse throughout the study with a total of 147 different species, varieties and forms being observed. As usual, diatoms predominated with 117 taxa, followed by the Cyanophyta with 20, the Chlorophyta

Table 11. List of epilithic algae collected from the River Wylye which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata

Achnanthes minutissima v. *cryptocephala*

Amphora ovalis v. *pediculus*

Cocconeis placentula v. *euglypta*

Melosira varians

Nitzschia palea

Nitzschia palea v. *debilis*

Opephora martyi

Synedra ulna

Oscillatoria brevis

Phormidium foveolarum

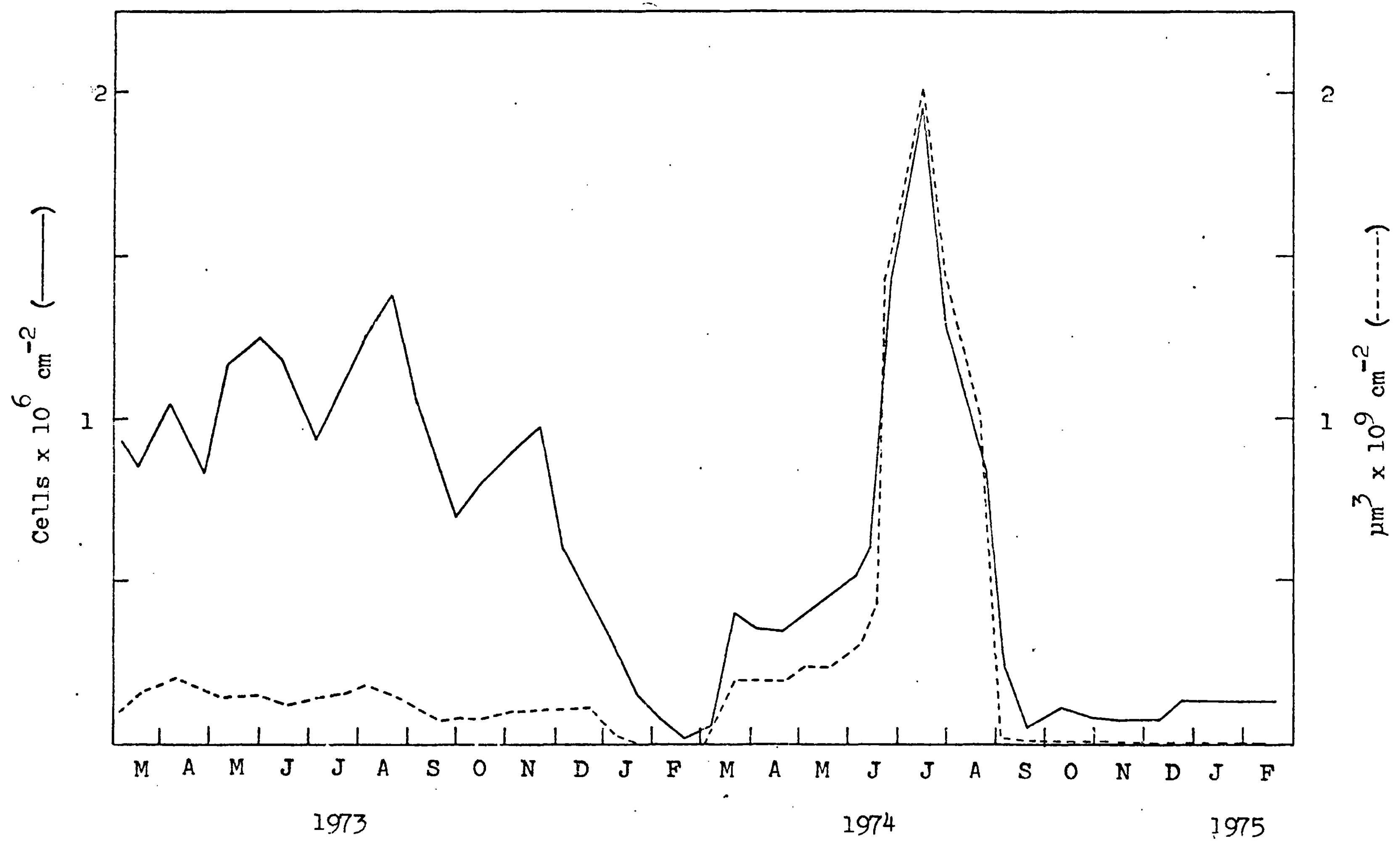

Fig. 27. Seasonal changes in the standing crop of the entire epilithic assemblage in the River Wylye.

with eight and the Euglenophyta with two. The most common diatoms were Nitzschia palea, Achnanthes minutissima v. cryptocephala, Nitzschia linearis and Melosira varians while Oscillatoria brevis and Phormidium foveolarum were the predominant cyanophytes (Table 12, Fig. 28). Both the Chlorophyta and Euglenophyta remained comparatively rare, the predominant species being Scenedesmus quadricauda, S. obliquus and Euglena sp.

The standing crop of the epilithic algae fell continuously as the distance from the water cress beds increased with values, for example, at the upper most collection area usually being 150 - 200% greater than those from the downstream site. Since, however, the proportion of the different taxa remained more or less homogeneous over the entire area, the data for the four sites were pooled. Thus, although the abundance of the different species generally exhibited a recurring pattern of seasonal abundance, considerable differences existed in the actual numbers of these algae in the two sampling years. For example, Nitzschia palea and varieties, N. linearis, Melosira varians and Synedra acus exhibited a high degree of development during April 1974 compared with 1973, whereas the opposite pattern was observed in the case of Achnanthes minutissima v. cryptocephala (Fig. 28). Of the ten most common taxa in the community, only Oscillatoria brevis showed a highly consistent pattern of seasonal abundance. During 1973, this species reached peak abundance, 6.75×10^6 filaments cm^{-2}, near the middle of May, virtually the same time as the peak, 9.0×10^6 filaments cm^{-2}, was attained in 1974.

The total assemblage began to develop markedly in April when the standing crop initially averaged 6×10^6 cells cm^{-2} (Fig. 29). By the beginning of May the density had increased to 44×10^6 cells cm^{-2} after which the numbers fell sharply. The community remained relatively well developed during the winter with a precipitous upsurge in numbers to 58.2×10^6 cells cm^{-2} taking place in April. Thereafter, the community waned dramatically but with relatively constant numbers being maintained from August until February 1975. Seasonal changes in the standing crop of the flora in terms of cell volume paralleled those outlined above. The highest recorded density, 52.3×10^9 μm^3 cm^{-2} in 1973, was in May while in 1974 peak algal abundance, 65.1×10^9 μm^3 cm^{-2}, was found during April. The daily growth rate of the community was much

Table 12. List of epilithic algae collected from a tributary of the River Wylye which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Achnanthes minutissima v. *cryptocephala*
Cymbella affinis
Cymbella caespitosa
Cymbella ventricosa
Diatoma vulgare v. *breve*
Fragilaria capucina v. *lanceolata*
Fragilaria intermedia
Fragilaria leptostauron
Gomphonema olivaceum
Gomphonema olivaceum v. *minutissima*
Gomphonema parvulum
Melosira varians
Meridion circulare
Navicula cryptocephala v. *veneta*
Navicula pelliculosa
Navicula tripunctata
Nitzschia fonticola
Nitzschia linearis
Nitzschia palea
Nitzschia palea v. *debilis*
Opephora martyi
Surirella ovata v. *minuta*
Synedra acus
Synedra minusculus
Synedra ulna
Synedra ulna v. *oxyrhynchus*
Oscillatoria brevis
Phormidium foveolarum

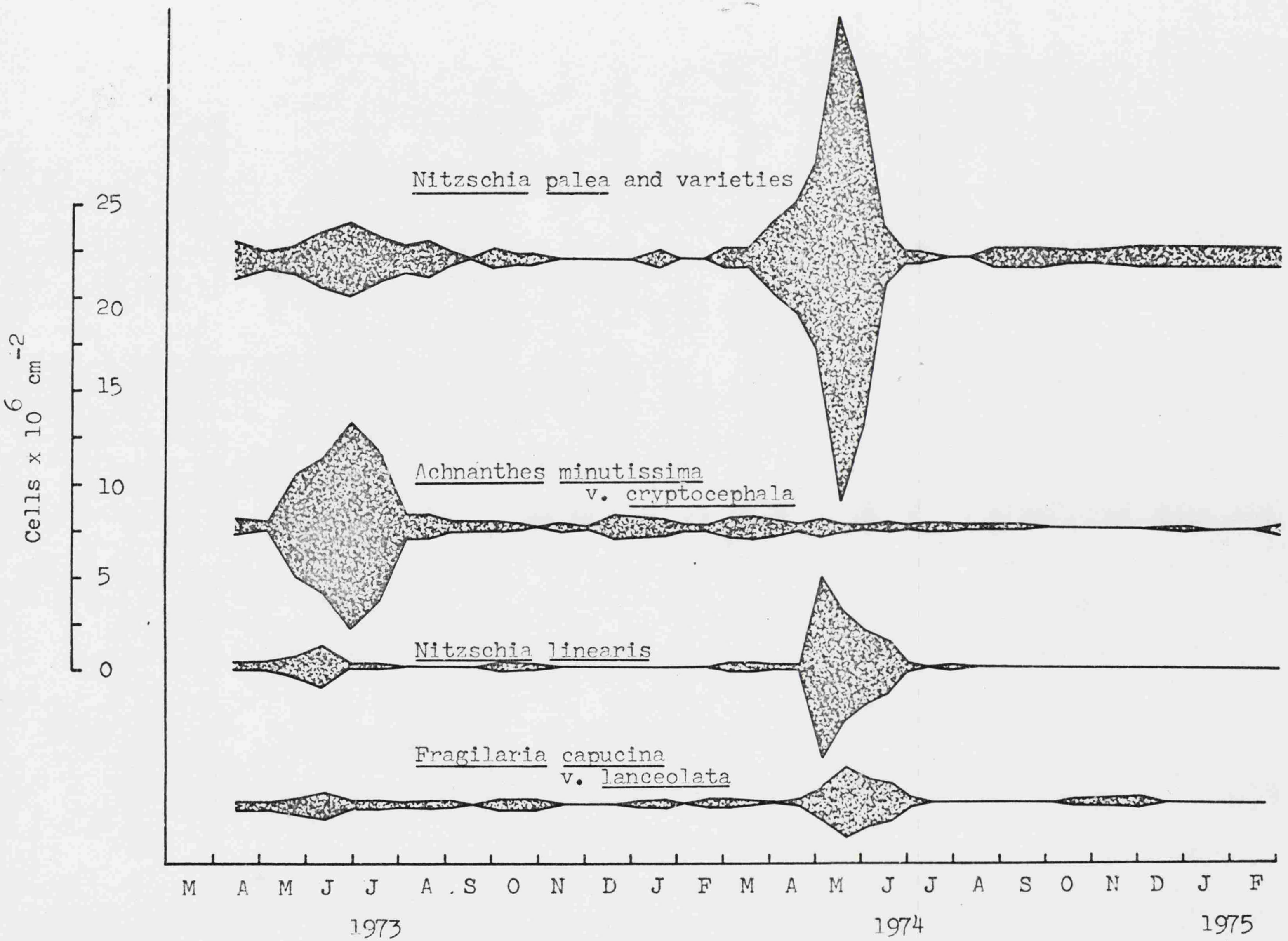

Fig. 28. Seasonal changes in the standing crop of common epilithic algae in the tributary of the River Wylye.

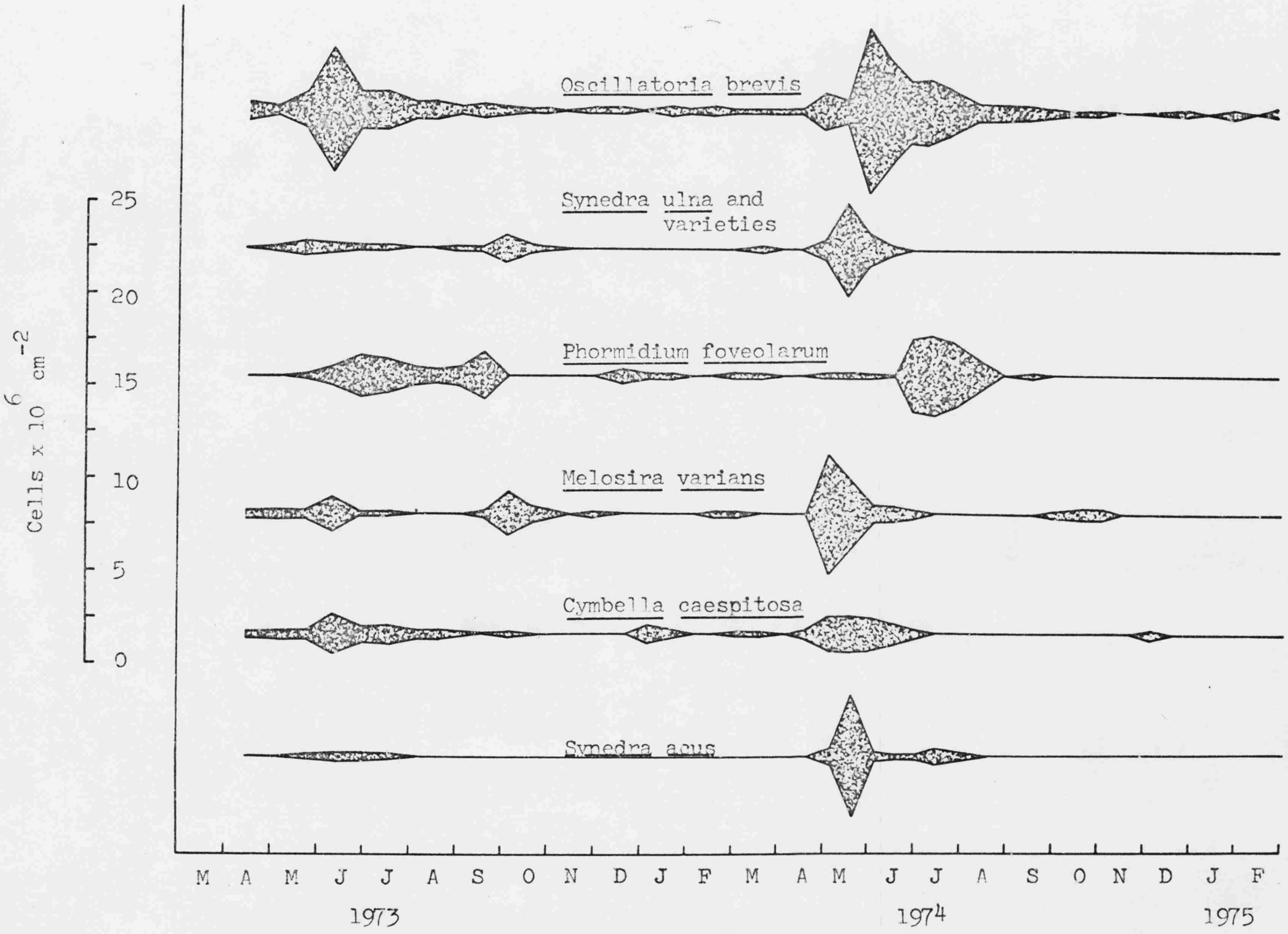

Fig. 28 (Cont'd). Seasonal changes in the standing crop of common epilithic algae in the tributary of the River Wylye.

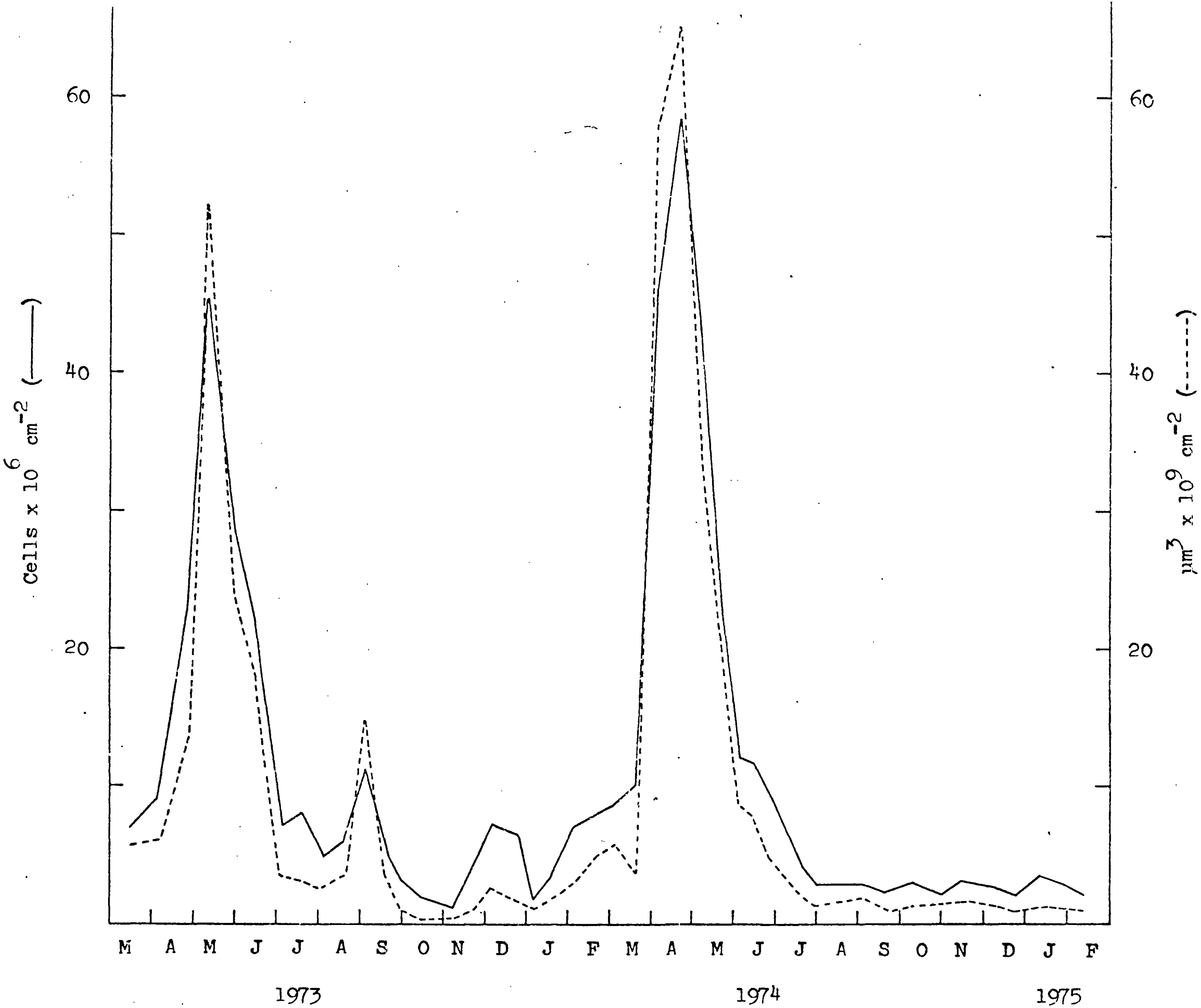

Fig. 29. Seasonal changes in the standing crop of the entire epilithic assemblage in the tributary of the River Wylye.

faster than that exhibited by either the epipelic or episammic flora (Fig. 29). For example, during 1973 maximum values of 1.47×10^6 cells cm^{-2} and 2.5×10^9 μm^3 cm^{-2} were observed in May while in 1974 at the beginning of April even higher values of 2.4×10^6 cells cm^{-2} and 3.6×10^9 μm^3 cm^{-2} were found. In 1973, the greatest daily disappearance rate of the algae from the community, 0.85×10^6 and 0.75×10^6 cells cm^{-2}, occurred during May and June respectively. In May 1974, however, even higher daily disappearance rates, e.g. 1.0×10^6 cells cm^{-2}, were recorded.

Potamoplankton and the Planktonic Communities

Approximately 200 different kinds of diatoms were found floating in the mainstream of the River Wylye, together with 26 chlorophytes, 13 cyanophytes, four euglenophytes and one chrysophyte. The most frequently encountered members of the first group included *Achnanthes lanceolata*, *A. minutissima* v. *cryptocephala*, *Nitzschia linearis*, *N. palea* and *Melosira varians* while *Chlamydomonas monadina* and *Scenedesmus obliquus* were the predominant chlorophytes (Table 13). The other three major Divisions were normally poorly represented, the most common species being *Trachelomonas volvocina*, *Phormidium foveolarum* and *Dinobryon sertularia*.

In terms of numbers, the true planktonic species represented from5 to 40% of the algae floating in the water. The most common species in this group, *Chlamydomonas monadina*, showed some development, i.e. 3 - 5% of the total flora during November and December of 1973, but the highest proportions, i.e. 15 - 33%, occurred between June and September 1974. Much the same pattern of succession was exhibited by another unidentified species of *Chlamydomonas*, but the relative abundance of this taxon never exceeded 10.5% and was usually much less. In contrast to the above patterns, *Scenedesmus* spp. (mainly *S. obliquus*, *S. bijuga* and *S. quadricauda*) showed maximum development during September 1973 when they accounted for approximately 15% of the total algal flora, but at other times remained comparatively restricted. Planktonic diatoms, mainly *Cyclotella comta* and *Stephanodiscus hantzschii*, seldom accounted for more than 3% of the algae.

The standing crop of the entire assemblage varied tremendously during the two years of the investigation (Fig. 30). For example,

Table 13a. List of algae floating in the River Wylye which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Achnanthes minutissima v. *cryptocephala*
Amphora ovalis v. *pediculus*
Fragilaria capucina v. *lanceolata*
Gomphonema constrictum
Melosira varians
Meridion circulare
Nitzschia linearis
Nitzschia palea
Nitzschia palea v. *debilis*
Opephora martyi
Chlamydomonas sp.
Chlamydomonas monadina
Scenedesmus obliquus
Phormidium foveolarum

Table 13b. List of planktonic algae collected from the River Wylye which accounted for between 1 and 10% of the flora on at least one sampling date.

Cyclotella comta
Stephanodiscus hantzschii
Ankistrodesmus falcatus
Pediastrum duplex
Scenedesmus bijuga
Scenedesmus quadricauda
Selenastrum gracile
Dactylococcopsis smithii
Trachelomonas sp.
Trachelomonas volvocina

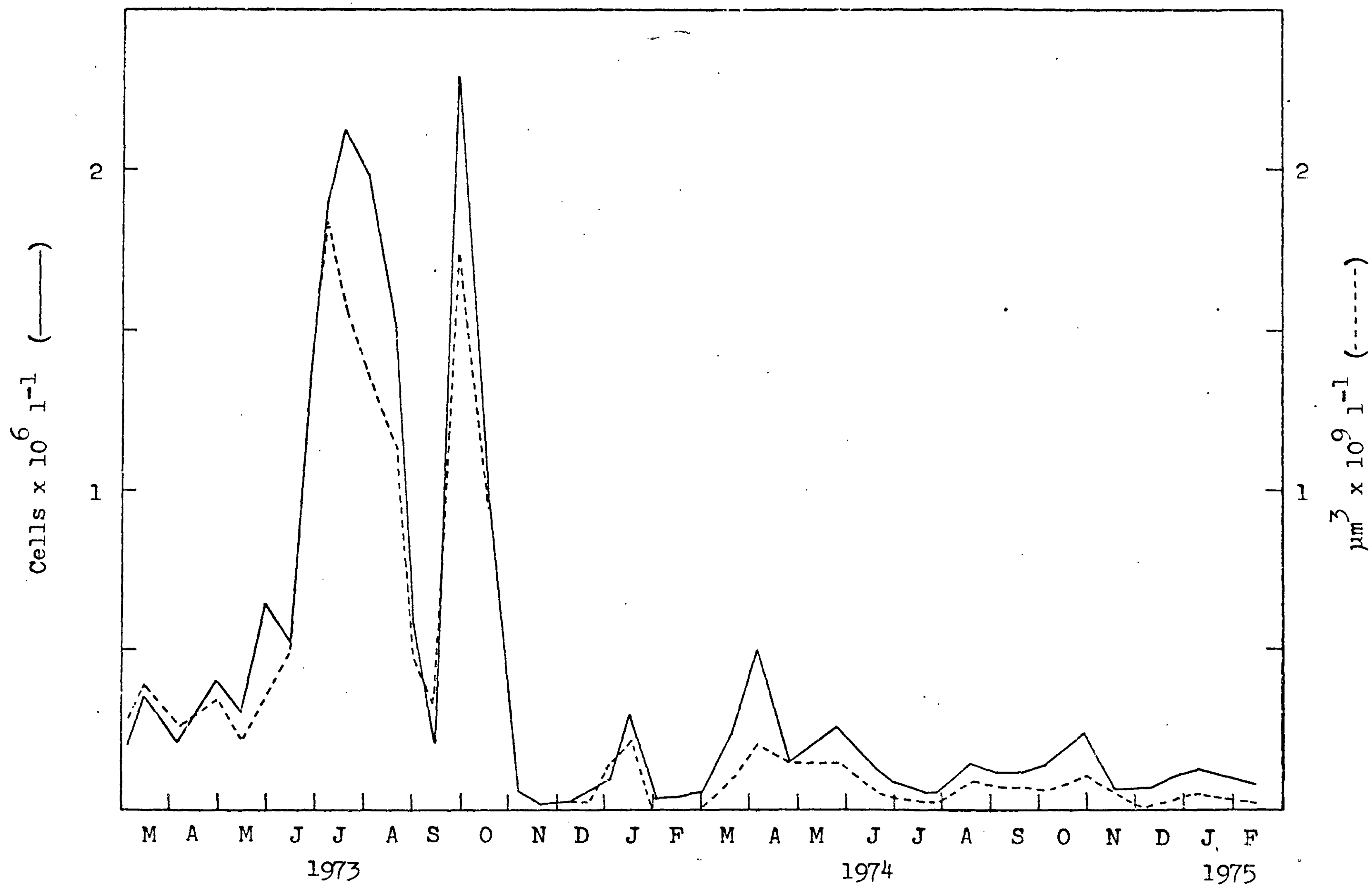

Fig. 30. Seasonal changes in the standing crop of the entire algal assemblage floating in the River Wylye.

in the warmer months of 1973, the number of cells ranged from 0.5 x 10^6 to 2.3 x 10^6 l^{-1} (0.5 - 1.8 x 10^9 μm^3 l^{-1}) while in 1974 the corresponding value was 0.5 - 5.0 x 10^5 cells l^{-1} (0.2 - 2.0 x 10^8 μm^3 l^{-1}). As the discharge in both summers was similar (Fig. 20), these differences were not apparently related to fluctuations in the volume of the river water. Seasonal change in the standing crop of the true planktonic species during 1973 was characterized by a well-defined peak of approximately 3.0 x 10^4 cells l^{-1} during September. In contrast, during 1974, a comparable upsurge in numbers was maintained throughout the summer.

The assemblage of algae found floating in the tributary was less diverse than that described for the main Wylye. Approximately 180 different species and varieties of diatoms were observed while 21 additional taxa belonged to the Chlorophyta, 12 to the Cyanophyta and four to the Euglenophyta. Many of the predominant species in these groups were similar to those in the main river but the true planktonic forms were more common (Table 14). *Chlamydomonas* sp. and *C. monadina*, for example, normally occurred throughout the investigation, the two together representing from 3 to 20% of the total algal flora. Similarly, *Cyclotella comta*, although rare in the summer, was recorded in large numbers (5 - 17%) during both winters while *Scenedesmus obliquus* showed considerable development (2 - 12%) during the spring and summer.

As with the Wylye, the standing crop of the entire assemblage was much higher during the warmer months of 1973 (0.2 - 1.9 x 10^6 cells l^{-1}; 0.15 - 1.3 x 10^9 μm^3 l^{-1}) than that of 1974 (0.1 - 4.5 x 10^5 cells l^{-1}; 0.06 - 2.2 x 10^8 μm^3 l^{-1}) and once again this feature is not apparently related to variation in discharge (Fig. 31). The general pattern of change in the tributary bore many similarities to that outlined for the main Wylye, particularly in the sharp rise in numbers that took place near the beginning of July 1973. Compared to the main river, the true plankton was always well developed with densities ranging from 0.4 x 10^5 cells l^{-1} in the winter to 1.2 x 10^5 cells l^{-1} in the summer.

Table 14a. List of algae floating in a tributary of the River Wylye which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Achnanthes minutissima v. cryptocephala
Cyclotella comta
Fragilaria capucina v. lanceolata
Fragilaria intermedia
Melosira varians
Meridion circulare
Nitzschia linearis
Nitzschia palea
Nitzschia palea v. debilis
Chlamydomonas monadina
Scenedesmus obliquus

Table 14b. List of planktonic algae collected from a tributary of the River Wylye which accounted for between 1 and 10% of the flora on at least one sampling date.

Stephanodiscus hantzschii
Ankistrodesmus falcatus
Chlamydomonas sp.
Scenedesmus armatus
Scenedesmus bijuga
Scenedesmus quadricauda

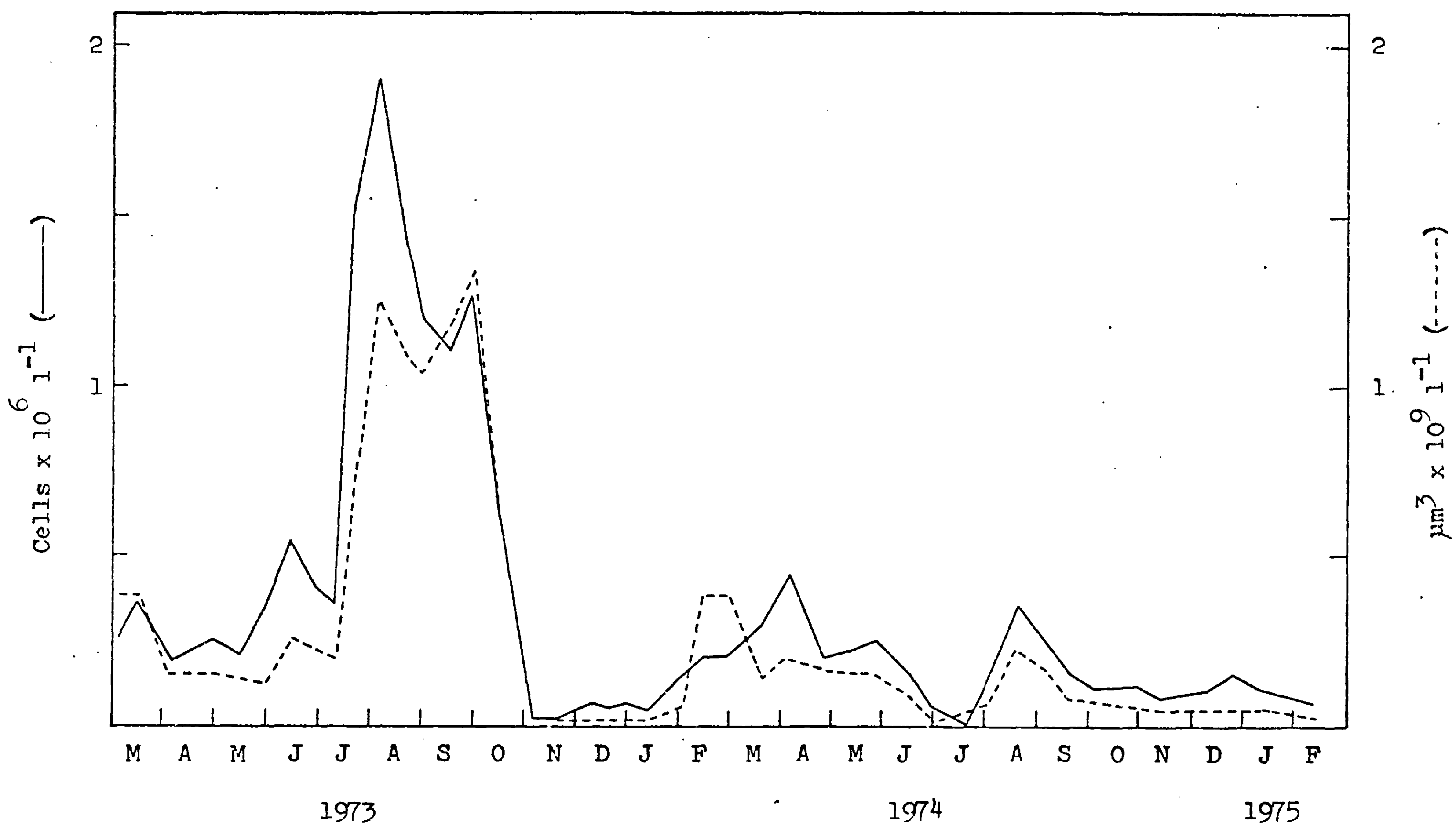

Fig. 31. Seasonal changes in the standing crop of the entire algal assemblage floating in the tributary of the River Wylye.

Epiphytic Communities

Approximately 220 different kinds of algae occurred on the water cress in the River Wylye, of which 210 belonged to the Bacillariophyta, six to the Chlorophyta and four to the Cyanophyta. The most common species were Achnanthes lanceolata and A. minutissima v. cryptocephala, followed in much reduced numbers by Cocconeis placentula and C. placentula v. euglypta (Table 15; Fig. 32). Although achieving considerable development in some instances, the other forms listed in Table 15 normally occurred only in small numbers. The abundance of Achnanthes lanceolata remained relatively constant during much of 1973 with an average density of 2.8×10^5 cells cm^{-2}. During November and December, however, this species waned significantly. Thereafter, the standing crop increased to $2.0 - 6.2 \times 10^5$ cells cm^{-2} but there appeared to be little consistent pattern of variation in the abundance of this species, although it did decline markedly in the winter. Much the same trend was exhibited by Achnanthes minutissima v. cryptocephala but the size of the standing crop and its seasonal fluctuations tended to be greater than that outlined for A. lanceolata. Only two other species of algae, Cocconeis placentula and C. placentula v. euglypta, occurred in large numbers of the water cress and, as with the more common forms, recurring patterns of seasonal abundance were not observed.

The standing crop of the entire assemblage exhibited only a small degree of variation during most of 1973, the average value being about 1.3×10^6 cells cm^{-2} (Fig. 33). Although numbers fell to 0.5×10^5 cells cm^{-2} in November, the assemblage started to show improved development in January 1974. As with 1973, only relatively small fluctuations were found in the seasonal abundance during the whole of 1974. Paralleling the density values, no spring upsurge was observed in cell volume during either 1973 or 1974. In the spring of 1973 the standing crop averaged 0.4×10^9 μm^3 cm^{-2} and showed little variation. It did, however, rise abruptly during the summer to 1.15×10^9 μm^3 cm^{-2}, but thereafter, the community waned although showing a sharp increase to over 0.6×10^9 μm^3 cm^{-2} in December and January. A gradual increase in abundance then took place with values reaching 0.9×10^9 μm^3 cm^{-2} by April.

The fastest daily growth rates in numbers occurred during the winter

Table 15. List of epiphytic algae associated with water cress in the River Wylye which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata

Achnanthes lanceolata f. *ventricosa*

Achnanthes minutissima v. *cryptocephala*

Cocconeis placentula

Cocconeis placentula v. *euglypta*

Eunotia valida

Gomphonema olivaceum v. *balticum*

Gomphonema parvulum

Nitzschia palea

Nitzschia palea v. *debilis*

Opephora martyi

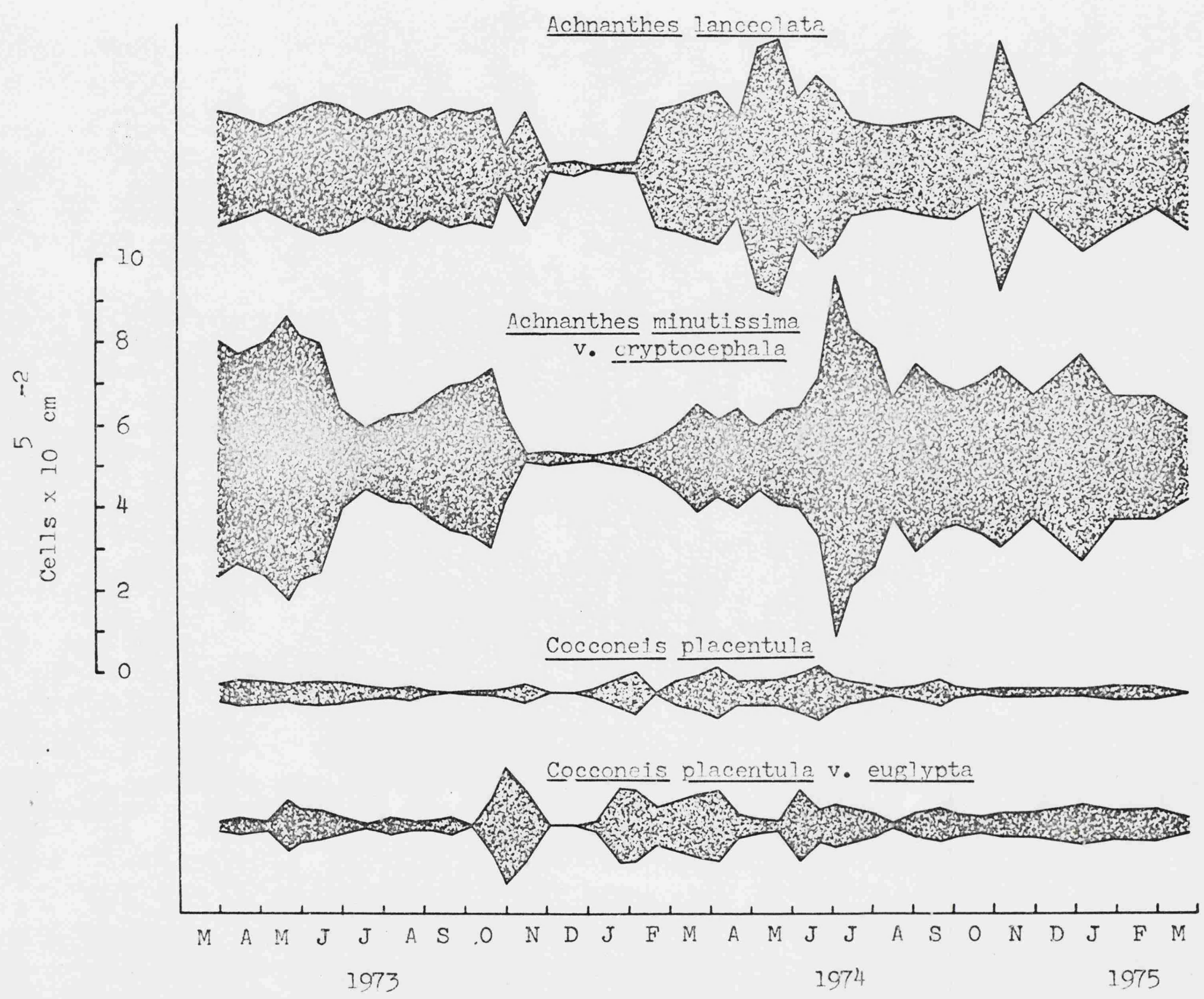

Fig. 32. Seasonal changes in the standing crop of common algae epiphytic upon water cress in the River Wylye.

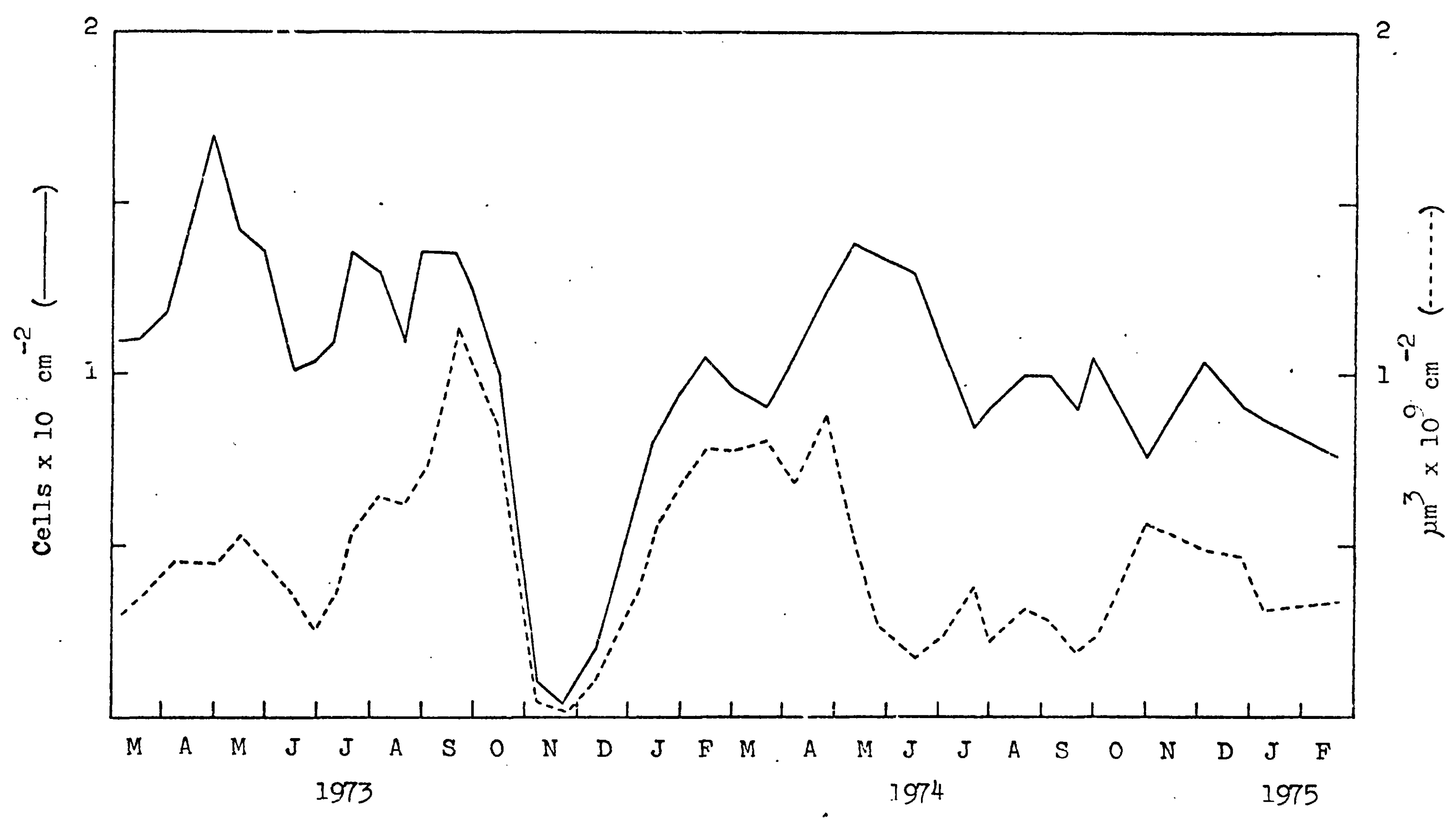

Fig. 33. Seasonal changes in the standing crop of the entire algal assemblage epiphytic upon water cress in the River Wylye.

of 1973 - 1974 when values of 1.5 - 2.0 x 10^4 cell cm^{-2} were recorded while, in terms of volume the highest value, 2.0 x 10^7 μm^3 cm^{-2}, occurred in September 1973. At other times of the year, even during the spring, the maximum rate of recruitment seldom exceeded 50% of the above levels. Algae disappeared from the water cress most quickly during October 1973 when a daily value of 4.5 x 10^4 cells cm^{-2} was observed, while the second fastest rate, 2.3 x 10^4 cells cm^{-2}, occurred in May 1973

The diversity of the flora found in association with Cladophora glomerata was similar to that outlined above for the water cress epiphytes. Diatoms once again predominated with 178 species followed by the Chlorophyta with 22, the Cyanophyta with 13 and Euglenophyta with five. The most common members of the first group of algae were Achnanthes lanceolata, A. minutissima v. cryptocephala, Diatoma vulgare, Gomphonema olivaceum and Meridion circulare while Scenedesmus obliquus and S. quadricauda were the important chlorphytes (Table 16; Fig. 34). The Cyanophyta were most frequently represented by Chamaesiphon incrustans and Oscillatoria limosa while Euglena sp. was the dominant euglenoid.

The predominant species generally failed to show well-defined recurring seasonal patterns in abundance. Achnanthes lanceolata and most other species showed at least some development throughout the study but attained relatively high peaks in abundance at only one point during the investigation (Fig. 34). Achnanthes minutissima v. cryptocephala on the other hand occurred abundantly most of the time but on several brief occasions exhibited a sharp drop in numbers. Gomphonema olivaceum and varieties were the only taxa to show a clear recurring seasonal pattern in peak densities with values of approximately 1.6 x 10^7 and 1.4 x 10^7 cells g^{-1} being recorded in September of 1973 and 1974 respectively.

As with the epiphytes attached to water cress, a well-defined spring upsurge in numbers failed to occur on Cladophora during both 1973 and 1974. The standing crop fluctuated a great deal during the first part of the investigation ranging from approximately 6 x 10^6 cells g^{-1} in May to 39 x 10^6 cells g^{-1} in July. A sharp drop in numbers occurred during the autumn (1 x 10^6 cells g^{-1} in November)

Table 16. List of epiphytic algae associated with *Cladophora glomerata* in the tributary of the River Wylye which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Achnanthes lanceolata v. *dubia*
Achnanthes minutissima v. *cryptocephala*
Amphora ovalis v. *pediculus*
Cymbella caespitosa
Diatoma vulgare
Diatoma vulgare v. *producta*
Fragilaria capucina v. *lanceolata*
Gomphonema olivaceum
Gomphonema olivaceum v. *balticum*
Meridion circulare
Melosira varians
Nitzschia fonticola
Synedra ulna

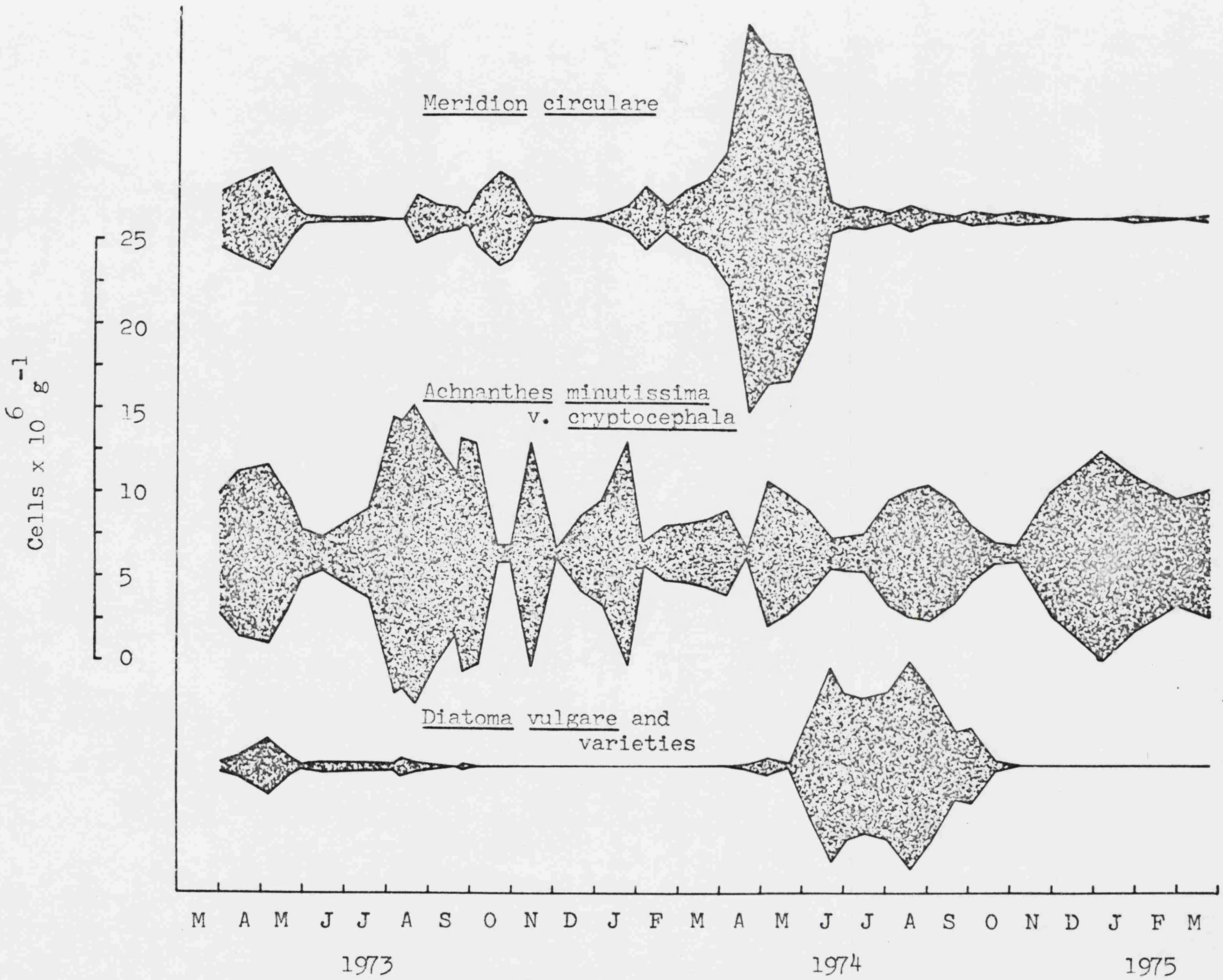

Fig. 34. Seasonal changes in the standing crop of common algae epiphytic upon <u>Cladophora glomerata</u> in the tributary of the River Wylye.

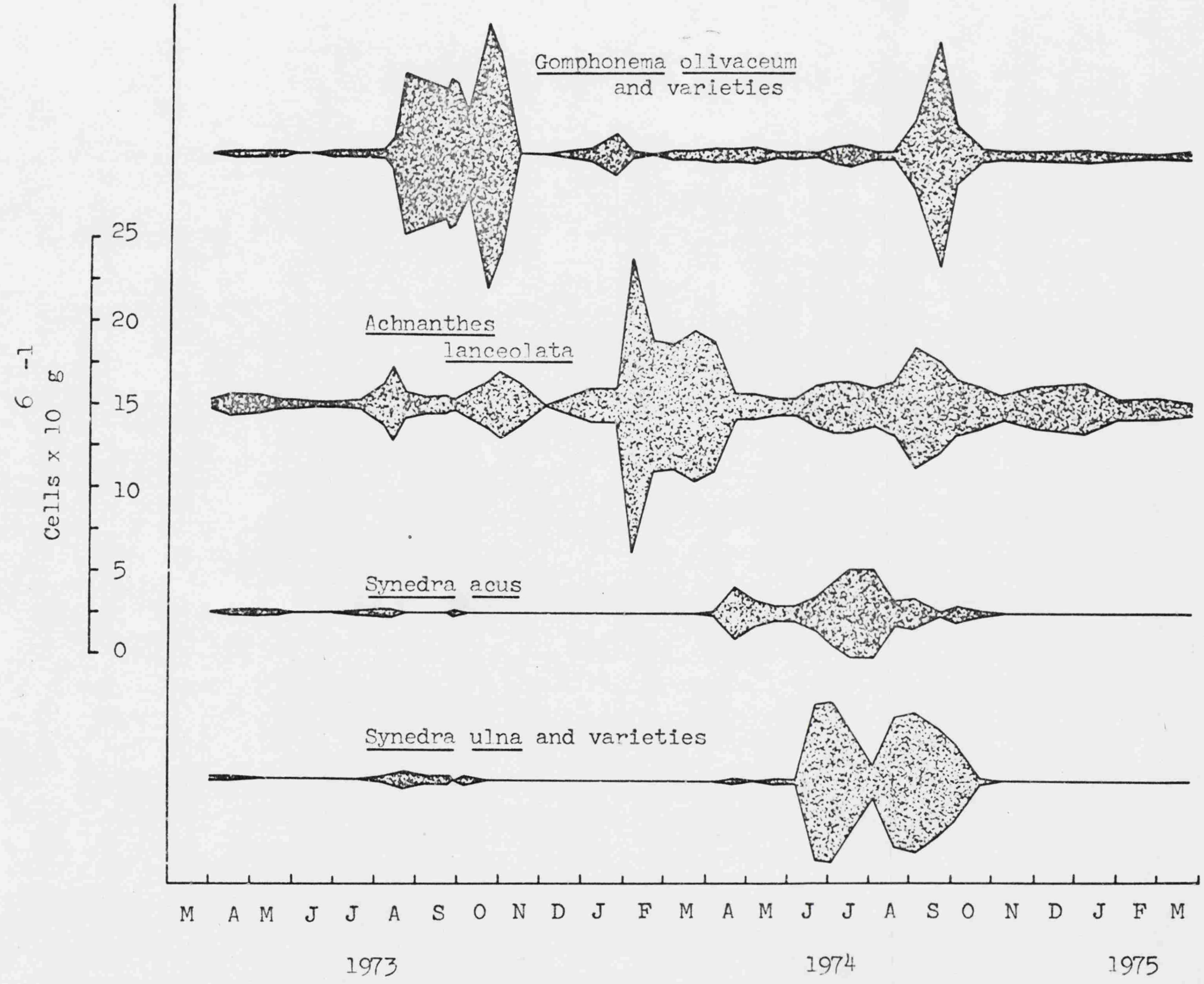

Fig. 34 (Cont'd). Seasonal changes in the standing crop of common algae epiphytic upon *Cladophora glomerata* in the tributary of the River Wylye.

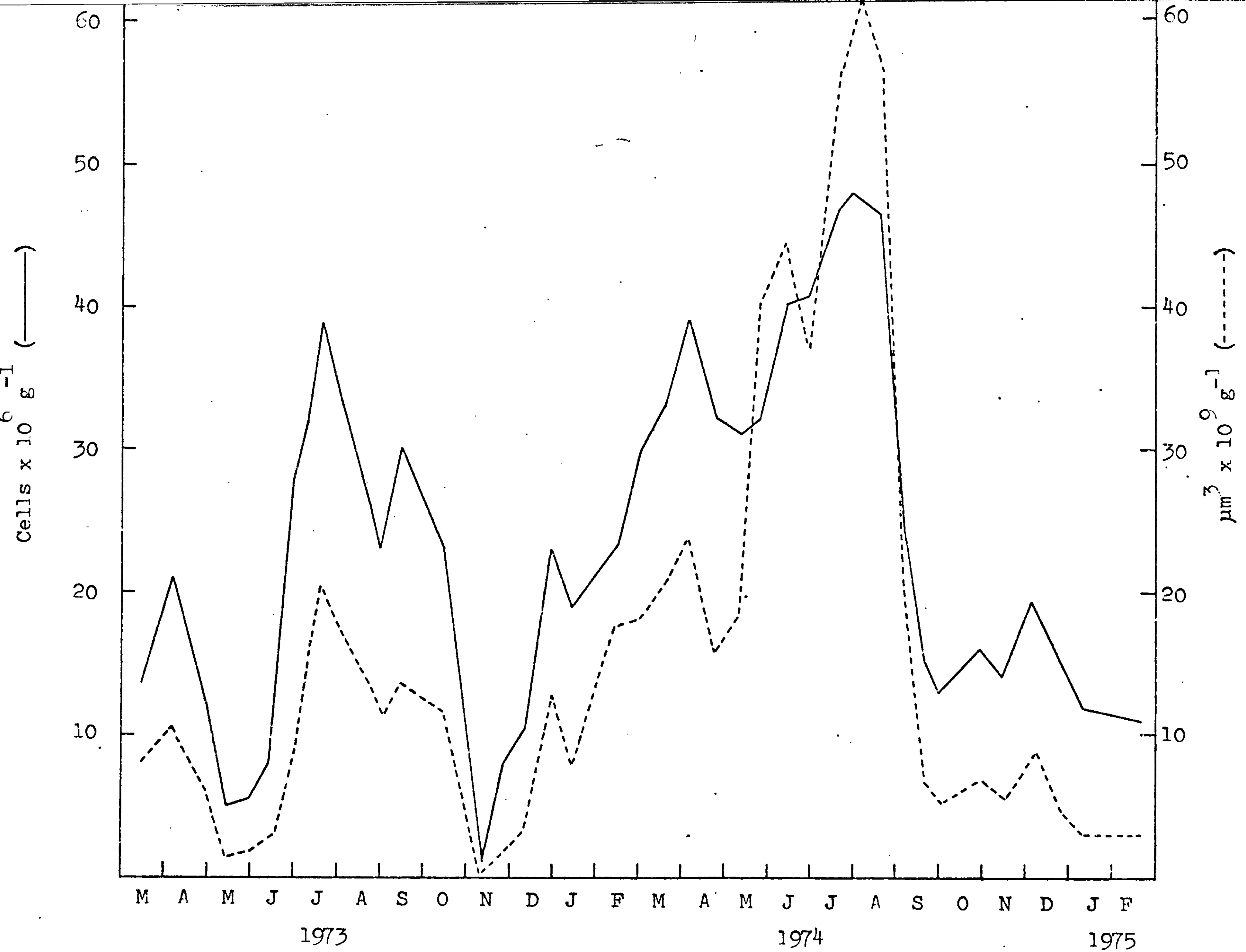

Fig. 35. Seasonal changes in the standing crop of the entire algal assemblage epiphytic upon <u>Cladophora glomerata</u> in the tributary of the River Wylye.

but thereafter the amount of algae increased erratically to 48 x 10^6 cells g^{-1} by August. The standing crop then fell sharply leveling off at 10 - 20 x 10^6 cells g^{-1} for the remainder of the investigation. Seasonal changes in the amount of algae in terms of cell volume almost exactly paralleled those outlined for numbers. The maximum daily rate of development in terms of numbers, 1.3 x 10^6 cells g^{-1}, took place during June 1973 while in 1974 the fastest rate, 0.4 x 10^6 cells g^{-1}, occurred in March. In terms of cell volume, the greatest daily rates, 1.5 x 10^9 and 0.95 x 10^9 μm^3 g^{-1}, were observed during May and July of 1974 respectively, while in 1973, the maximum daily rate was 0.7 x 10^9 μm^3 g^{-1} recorded in June. Algae disappeared from Cladophora at a maximum daily rate of 2.1 x 10^6 cells g^{-1} during August 1974 followed by a value of 0.9 x 10^6 cells g^{-1} towards the beginning of November 1973.

Discussion

The fact that the initial expansion of the epipelic community in both the Wylye and its tributary took place during March, following a period of increasing day length and coincident with similar development in the Avon, again indicates that light is probably an important factor influencing algal growth in rivers. As with the other streams investigated, periodic flooding enhanced algal growth during 1973, while in 1974 the invariably low discharge rates were correlated with low standing crops. It should be noted, however, that in two periods during 1973 algae disappeared at exceptionally high rates from the sediments of both the Wylye and its tributary. Since the first of these occasions was in May and June, coincident with flooding, it can be safely assumed to be correlated with the effects of high discharge rates. By contrast, the second drop in numbers occurred in September after a period of high standing crop and low water levels, suggesting that in this case the large scale detachment might, as in the Avon, be related to a high level of metabolic activity. Algal growth in the tributary was always greater than that in the main river, a feature presumably related to the fact that fertilizers were often added to the water cress beds upstream.

The species composition of the episammic community was similar to that described for other such communities from diverse bodies of water (Round, 1965; Moss and Round, 1967; Hickman, 1974b), a homogeneity that is perhaps surprising in view of the vast difference in environmental conditions in these studies. This suggests that sand grains tend always to provide a similar environment, while the limited number of species present indicates that only a few algae are well adapted to colonizing this type of habitat. Since sand grains can be easily disturbed by either current or wave action, poorly attached species would tend to be scoured away. This probably accounts for the relatively high proportion of *Amphora ovalis* v. *pediculus*, *Opephora martyi* and *Fragilaria construens* found in episammic communities, each of these species having a well developed attachment mechanism. At the same it should be noted that since *Cocconeis placentula* and *Rhoicosphenia curvata*, species also possessing considerable adhesive ability, are not present in any numbers, there must be some other factor limiting their ability to colonize this type of environment. Since many of the predominant species attached to sand grains are relatively small, this characteristic may enable them to find protection in crevices and hollows, a view previously suggested by Hickman (1974b). At least one of the predominant taxa in this investigation, Fragilaria construens, formed, however, comparatively long filaments which extruded from the substrate surface. In any consideration of episammic communities, it should be remembered that periods of extreme turbulence would tend to result in the burial of many members of the community. A characteristic common to all successful episammic species may therefore be their ability to withstand such conditions, a view supported by the presence in a lake investigated by Hickman (1974b) of large quantities of viable episammic flora, such as Amphora ovalis v. pediculus, Opephora martyi and Fragilaria construens, at depths of up to 10 cm from the sediment surface.

The absence of a well defined spring bloom in the episammic community of the tributary and the presence of the highest algal densities in the summer parallels the results of Hickman (1974b) for a community in the Canadian subarctic. The generally low standing crop and slow growth rates exhibited by the assemblage in the present study indicate either a slow photosynthetic rate or a high and continuous degree of detachment. The latter suggestion seems more likely as much of the episammic flora was frequently found in the potamoplankton. Algae disappeared, however, from the community at a slow rate compared with that examined by Hickman (1974b), a feature which he found (pers. comm.) was related to heavy wave action.

The highly restricted number of species as well as the density of the epilithic community in the Wylye parallels that found in other assemblages growing in rapid water (Dillard, 1971; Moore, 1974c). The generally low standing crop and growth rate of these algae is undoubtedly related to the fact that only a few species are adapted to fast flowing water. Phormidium foveolarum reached maximum density during the summer of 1974 coincident with the slowest rate of water flow recorded during the study, a finding which was unexpected in view of the observations of Fritsch (1929) which indicated that this species normally occurs in rapids. Possibly Phormidium was unable to compete for attachment sites with Amphora ovalis v. pediculus, a species which covered the stones during the period of faster water flow. This view is further substantiated by the fact that in the tributary where the water flow was slower and A. ovalis v. pediculus was far less abundant, P. foveolarum was always present in higher numbers than in the main Wylye. That Amphora is generally predominant in the main Wylye under conditions which do not show very marked fluctuations in discharge is presumably due to extremely successful adaptions to its epilithic mode of life. Furthermore, once established, other species clearly have difficulty in gaining a "foot hold" on these crowded substrates, a point made by Brook (1955a). However, one of the features of the epilithic community in the main Wylye is the relatively long period, i.e. about four months, that A. ovalis v. pediculus took to re - establish itself as the dominant algae following the floods of 1973 - 1974. Since other species successfully colonized the stone surfaces during this period, it would appear that, after the destruction of the original population by extreme conditions, Amphora cannot exhibit, until the spring or early summer, a sufficiently fast rate of growth to bring about exclusion of most other taxa.

The standing crop of the epilithic flora in the tributary was exceptionally high compared with values given in other studies (Gumtow, 1955; Douglas, 1958; Dillard, 1971; Evans and Stockner, 1973). This feature can almost certainly be related to the addition of fertilizers to the water cress beds upstream and also possibly to the production of growth inducing metabolic end products by the dense population of these macrophytes. This view is also consistent with the great abundance of Nitzschia palea in the tributary since this species is known to occur in large numbers in mesosaprobic areas (Butcher, 1947). The only epilithic species showing a consistent pattern of seasonal abundance in the two years was Oscillatoria brevis. This alga displayed peak numbers in the spring, a pattern which contrasted with the late summer and autumn peak recorded by Butcher et al. (1937) in a river in northern England.

The very high rates of disappearance of algae from the rocks during the periods of high standing crop in May 1973 can undoubtedly be attributed to the differences in the overall pattern of attachment by the algae with varying density. At most times of the year, when the algae formed a relatively thin layer over the substrate, the community can largely withstand normal water flows. During periods of increasing density, however, when the community produces a much thicker mass, the water flow will tend to dislodge algae more easily, since many will be attached to each other rather than to the stone substrate itself. This process may be exaggerated through the fact that the cells located at the base may tend to become senescent in dense populations (Moore, 1974b), thus further reducing the general attachment properties of the community as a whole. In addition, the large quantities of gas bubbles often found trapped among the mass of algae increase its buoyancy and further add to its susceptibility to the effects of water flow.

The absence of any significant development in the potamoplankton in the main Wylye and its tributary during the spring of both years can be correlated with the fact that since the community consisted mostly of detached diatoms, their numbers in the water depend largely on discharge rate and disturbances upstream rather than on an improvement in environmental conditions. As the standing crop in both areas during 1973 far exceeded that recorded in 1974, a pattern paralleling that exhibited by the epipelic communities but not by the epilithic flora, it seems likely that most of the potamoplankton was derived from the former of these assemblages. Although the rate of water flow in the Wylye normally ranged from 35 to 60 cm sec^{-1} , Chlamydomonas monadina and Scenedesmus spp. , which normally occur in much slower flowing water, developed substantial populations. Since, however, shoreline areas in the Wylye were often quiet, they permitted the growth of planktonic species and these then presumably became washed into the mainstream.

Since the standing crop of the entire assemblage on water cress dropped from high to negligible levels during November 1973 but thereafter increased sharply, paralleling changes in temperature, it appears that the shift in algal numbers was related to this factor. It is also important to note that the epiphytes associated with Cladophora glomerata in the tributary exhibited a comparable change in numbers at the same time thus further supporting the above suggestion. The increase in the standing crop of the epiphytes associated with Cladophora glomerata in the tributary during the spring and summer contrasts sharply with that exhibited by the epiphytes in the main Wylye. Direct microscopic examination of Cladophora indicated, however, that a considerable number of attachment sites were always available, a feature not observed in the case of the water cress. That the standing crop on Cladophora remained high during the winter compared to a similar assemblage in the Avon, reflects the addition of nutrients upstream on the growth of the epiphytic population.

Although large numbers of isopods and amphipods occurred in the Wylye, their grazing probably had little effect on the standing crop of the epilithic algae (Section 5). Since only a few representatives of these species occurred in the sediments of both the Wylye and its tributary they would likewise have had little effect on the epipelic community. Large numbers of copepods, mainly Cyclops sp.,occurred in the plankton of the tributary but, in all instances, their guts contained only detritus.

The Kennett and Avon Canal

In the vicinity of the collection sites (Lat. 51° 23' ; Long. 2° 19'), the Kennett and Avon Canal measured 30 m in width, one m in depth and flowed at a rate of about 7 - 12 cm sec^{-1}. Extensive growths of the bullrush, Typha latifolia L. , occurred along the bank while within 0 - 2 m of shore large quantities of water cress Nasturtium officinale R. Br. and pond weed Groenlandia densa (L.) Fourr. were observed. Free floating masses of filamentous algae, mainly Cladophora glomerata together with Spirogyra sp., occurred throughout the system. The surface of the water remained unshaded throughout the investigation but the filamentous algae had reduced the level of illumination at the sediment surface to less than 10 lux. This restriction severely limited the epipelic community and, as epilithic assemblages were never observed in the study area, the present investigation was concentrated on the planktonic and epiphytic forms. Water temperatures in the canal increased uniformly from 6 to 19.5°C between February and August 1973 but subsequently fell to 3 - 4 °C by November (Fig. 36). Values remained low throughout the winter ranging from 2.5 - 6.5°C but rising to 10°C by July. Although the water level varied, periods of flooding were never observed. The pH varied from 7.7 to 8.5 with the level of most nutrients remaining high (Table 17).

Planktonic Communities

Approximately 36 different kinds of truly planktonic algae were found in the canal, of which 9 belonged to the Bacillariophyta, 16 to the Chlorophyta, seven to the Euglenophyta and one to the Chrysophyta. The potamoplankton on the other hand was much more diverse, i.e. 186 taxa, with virtually all its members belonging to the former group of algae. The most common planktonic species were Chlamydomonas monadina and Trachelomonas volvocina v. minuta while Achnanthes minutissima v. cryptocephala, Nitzschia palea and Gomphonema olivaceum were the most frequently encountered detached forms (Table 18).

The abundance of Chlamydomonas monadina remained relatively constant at less than 1.6×10^4 cells l^{-1} during 1973 but between February and May 1974 increased to 1.0×10^5 cells l^{-1} (Fig. 37). Thereafter, the population waned sharply and failed to show any further

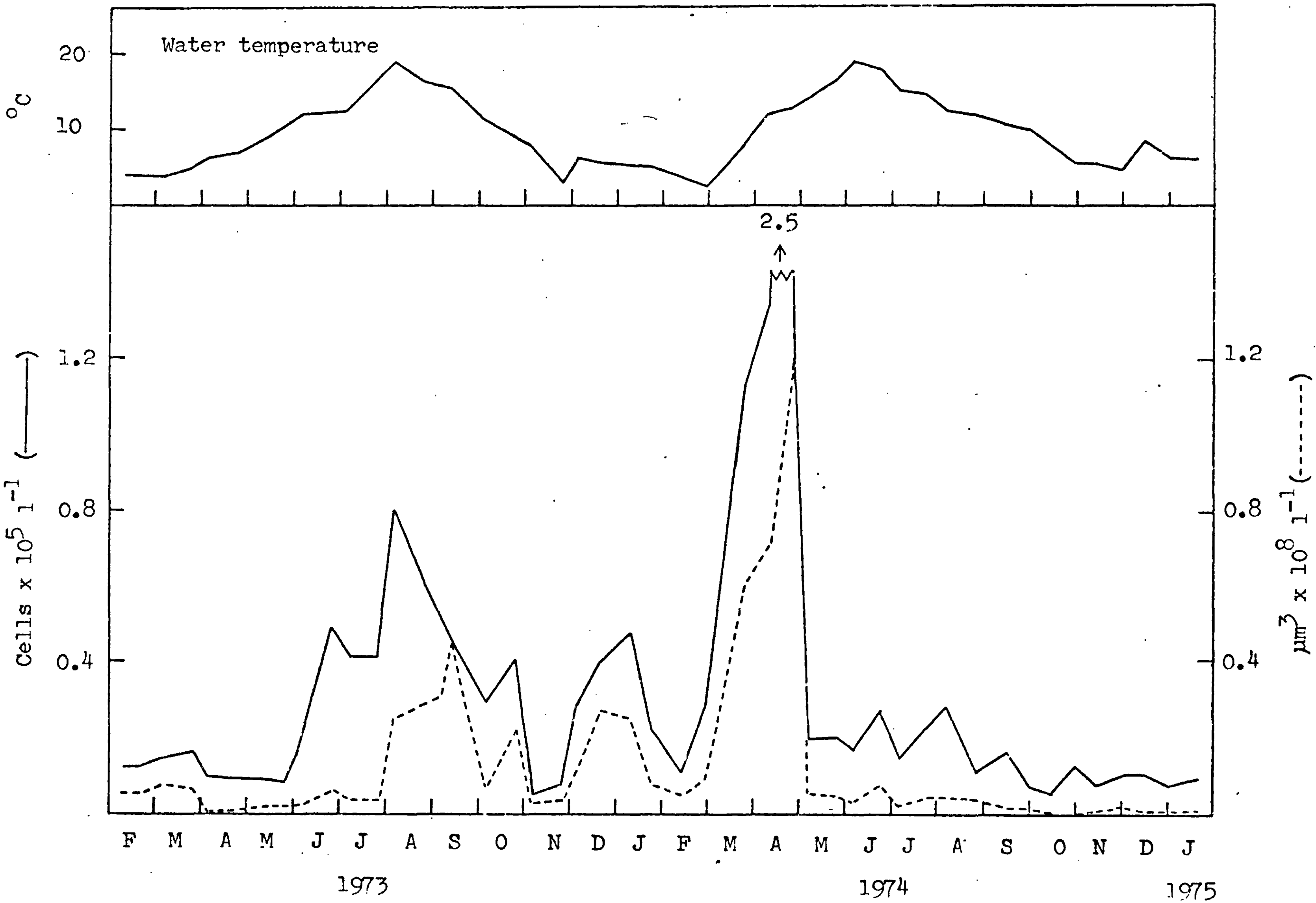

Fig. 36. Seasonal changes in the water temperature and in the standing crop of algae floating in the Kennett and Avon Canal.

Table 17. Physico-chemical properties of water from the Kennett and Avon Canal during 1973 and 1974. Except for pH, all data are expressed in terms of mg l^{-1}.

Parameter	Average	Range
pH	8.0	7.7 - 8.5
Total Alkalinity	292	240 - 395
Silica	4.2	2.1 - 6.5
Orthophosphate-Phosphorus	0.25	0.05 - 0.35
Nitrate-Nitrogen	3.1	2.4 - 6.9

Table 18a. List of algae floating in the Kennett and Avon Canal which accounted for at least 10% of the flora on at least one sampling date.

Achnanthes minutissima v. *cryptocephala*
Achnanthes lanceolata
Cocconeis placentula v. *euglypta*
Fragilaria capucina v. *lanceolata*
Fragilaria intermedia
Gomphonema olivaceum
Meridion circulare
Nitzschia palea
Chlamydomonas monadina
Trachelomonas volvocina v. *minuta*

Table 18b. List of planktonic algae collected from the Kennett and Avon Canal which accounted for between 1 and 10% of the flora on at least one sampling date.

Scenedesmus dimorphus
Stephanodiscus hantzschii
Chlamydomonas sp.
Trachelomonas volvocina

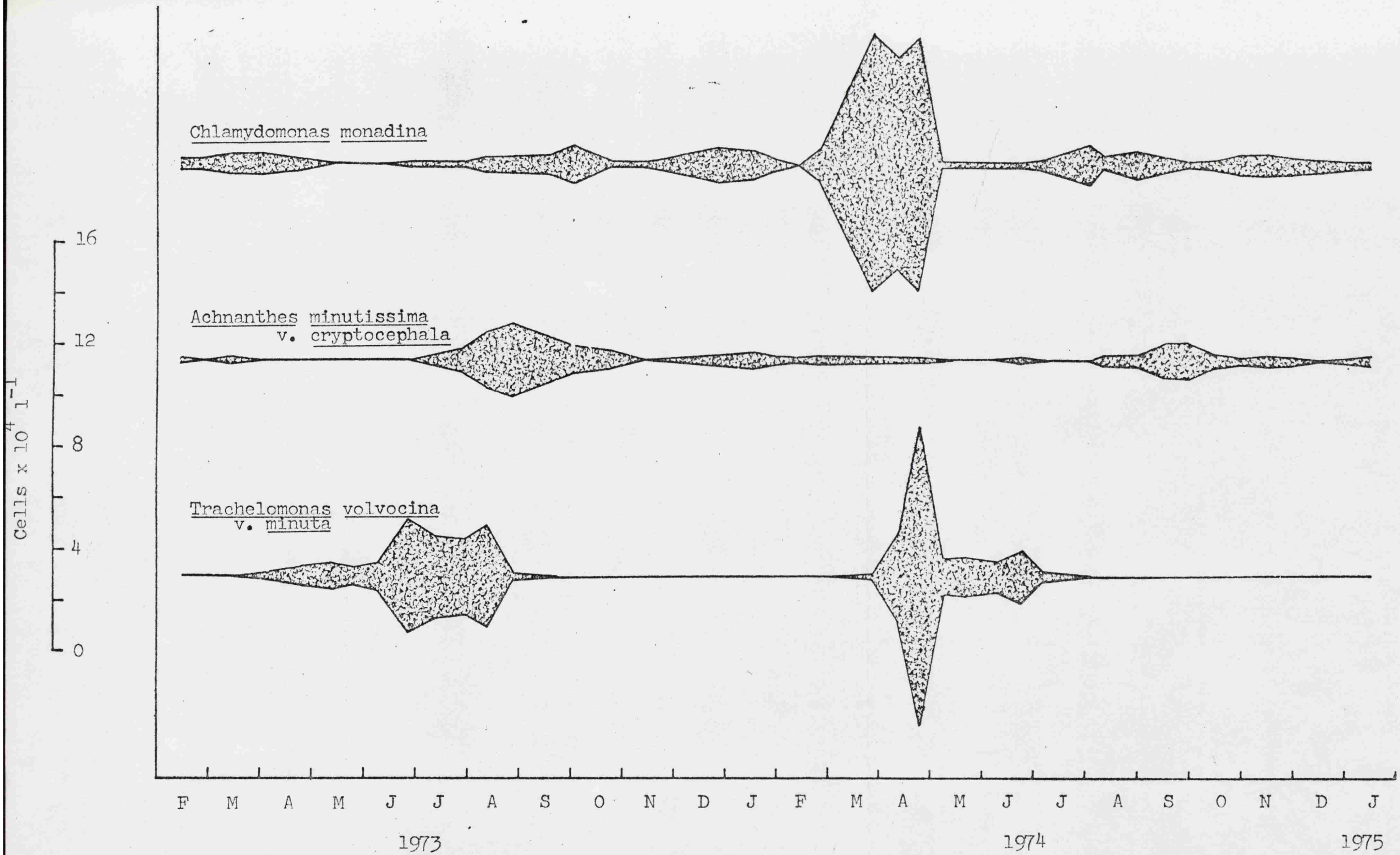

Fig. 37. Seasonal changes in the standing crop of common algae floating in the Kennett and Avon Canal.

increase. Trachelomonas volvocina v. minuta occurred in small numbers at the start of the investigation, but in March 1973 began to exhibit improved development reaching a maximum density of 3.0 - 4.5×10^4 cells l^{-1} during the summer with the population subsequently falling to low levels. During 1974, significant growth of the population began as early as April and, towards the end of this month, a density of 1.2×10^5 cells l^{-1} was recorded. The population then fell sharply and had virtually disappeared by August. The peak abundance of Achnanthes minutissima v. cryptocephala, the most common member of the potamoplankton, was reached during the late summer of both 1973 and 1974 when values of 2.8×10^4 and 1.2×10^4 cells l^{-1} respectively were recorded.

The standing crop of the entire assemblage remained comparatively restricted during the spring of 1973 but exhibited an increase during the summer when values of up to 0.8×10^5 cells l^{-1} (0.4×10^8 μm^3 l^{-1}) were obtained (Fig. 36). A relatively large population developed during the winter with a sharp increase in numbers (2.5×10^5 cells l^{-1}, 1.2×10^8 μm^3 l^{-1}) in March and April. The standing crop subsequently fell dramatically and remained low until the end of the investigation.

Epiphytic Communities

The algal assemblage found in association with Cladophora glomerata was comparatively diverse with 200 different species and varieties being recorded of which 187 belonged to the Bacillariophyta, eight to the Cyanophyta and five to the Chlorophyta. Achnanthes minutissima v. cryptocephala, which invariably predominated and accounted for at least 50 - 60% by numbers of the entire assemblage, did not show a recurring pattern of seasonal abundance. Several other species (Table 19), which occasionally achieved significant but brief importance, normally represented 2 - 6% of the flora.

The standing crop of the epiphytes increased to over 100×10^6 cells g^{-1} dry weight of Cladophora (50×10^9 μm^3 g^{-1}) during April 1973, with comparably high levels being maintained throughout the summer (Fig. 38). A depression in numbers occurred during the winter but in April an increase to over 230×10^6 g^{-1} (100×10^9 μm^3 g^{-1}) took place with values subsequently falling only to rise again in August. Thereafter, the standing crop fell and remained low until the end of the investigation.

Table 19. List of epiphytic algae associated with *Cladophora glomerata* in the Kennett and Avon Canal which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes minutissima v. *cryptocephala*

Cocconeis placentula

Cocconeis placentula v. *euglypta*

Gomphonema intricatum v. *pumilum*

Gomphonema olivaceum v. *balticum*

Rhoicosphenia curvata

Oscillatoria angustissima

Oscillatoria brevis

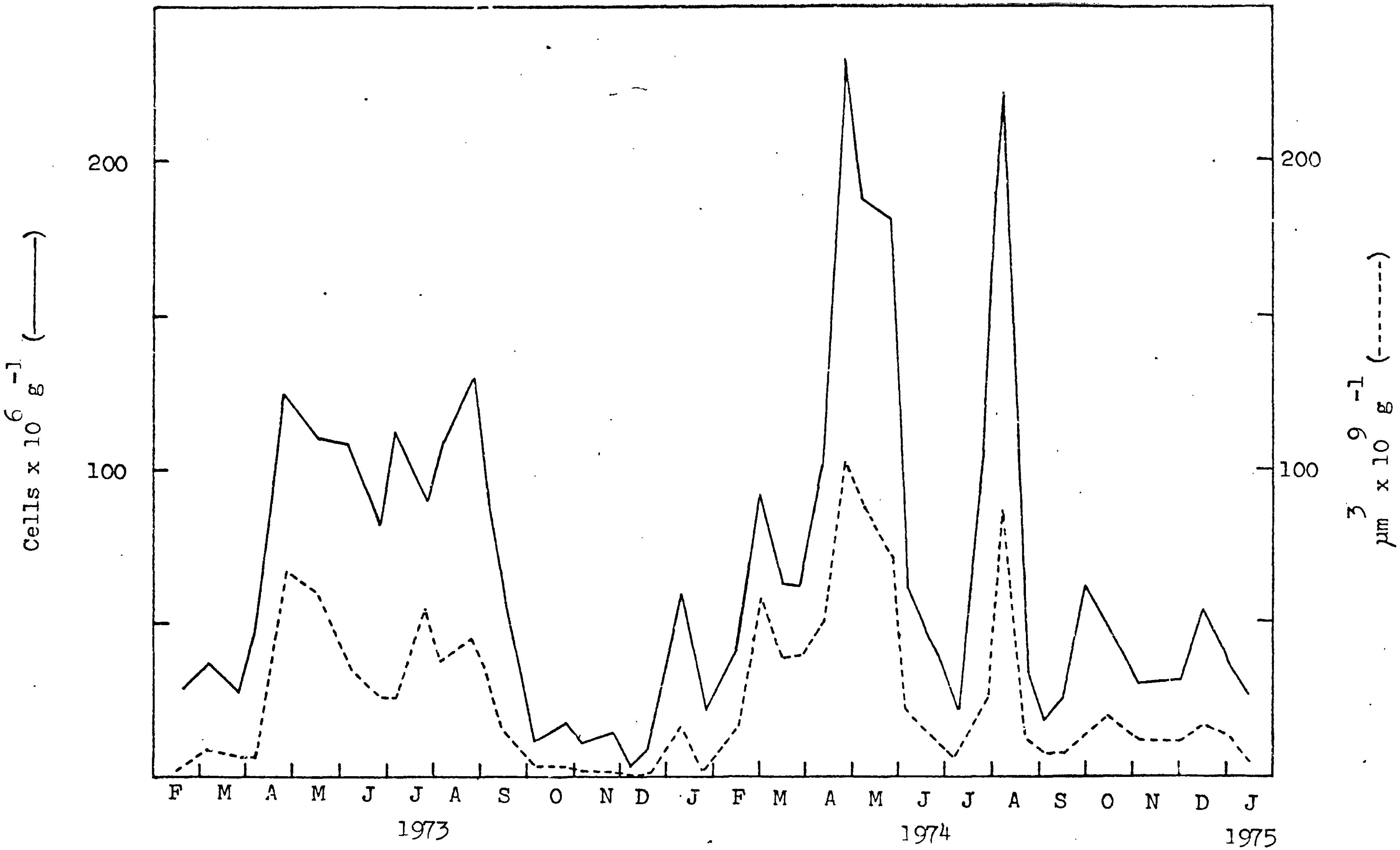

Fig. 38. Seasonal changes in the standing crop of the entire algal assemblage epiphytic upon *Cladophora glomerata* in the Kennett and Avon Canal.

Water cress supported 185 different kinds of algae of which 173 were diatoms, eight were cyanophytes and three were chlorphytes. Achnanthes minutissima v. cryptocephala was once again predominant throughout the year accounting for 50 - 80% of the flora. Cocconeis placentula and C. placentula v. euglypta were normally second in importance, each representing , on irregular occasions, 10 - 20% of the assemblage. Gomphonema olivaceum and G. olivaceum v. minutissima followed a similar pattern but the maximum relative abundance of these forms seldom exceeded 10%. The standing crop of the epiphytes usually remained relatively constant at about 1×10^6 cells cm^{-2}(0.4×10^9 μm^3 cm^{-2}) with maximum development ($1.5 - 2.2 \times 10^6$ cells cm^{-2}; 0.8×10^9 μm^3 cm^{-2}) occurring during the summer of both years (Fig. 39).

The assemblage of algae associated with the pond weed was virtually identical to that described for water cress. Achnanthes minutissima v. cryptocephala predominated, representing from 50 to 80% by numbers of the total community , followed in order of descending importance by C. placentula v. euglypta, C. placentula, G. olivaceum and G. olivaceum v. minutissima. The total standing crop of the community was slightly lower than that described for the water cress but peak values occurred once again during the summer of both 1973 and 1974 (Fig. 40).

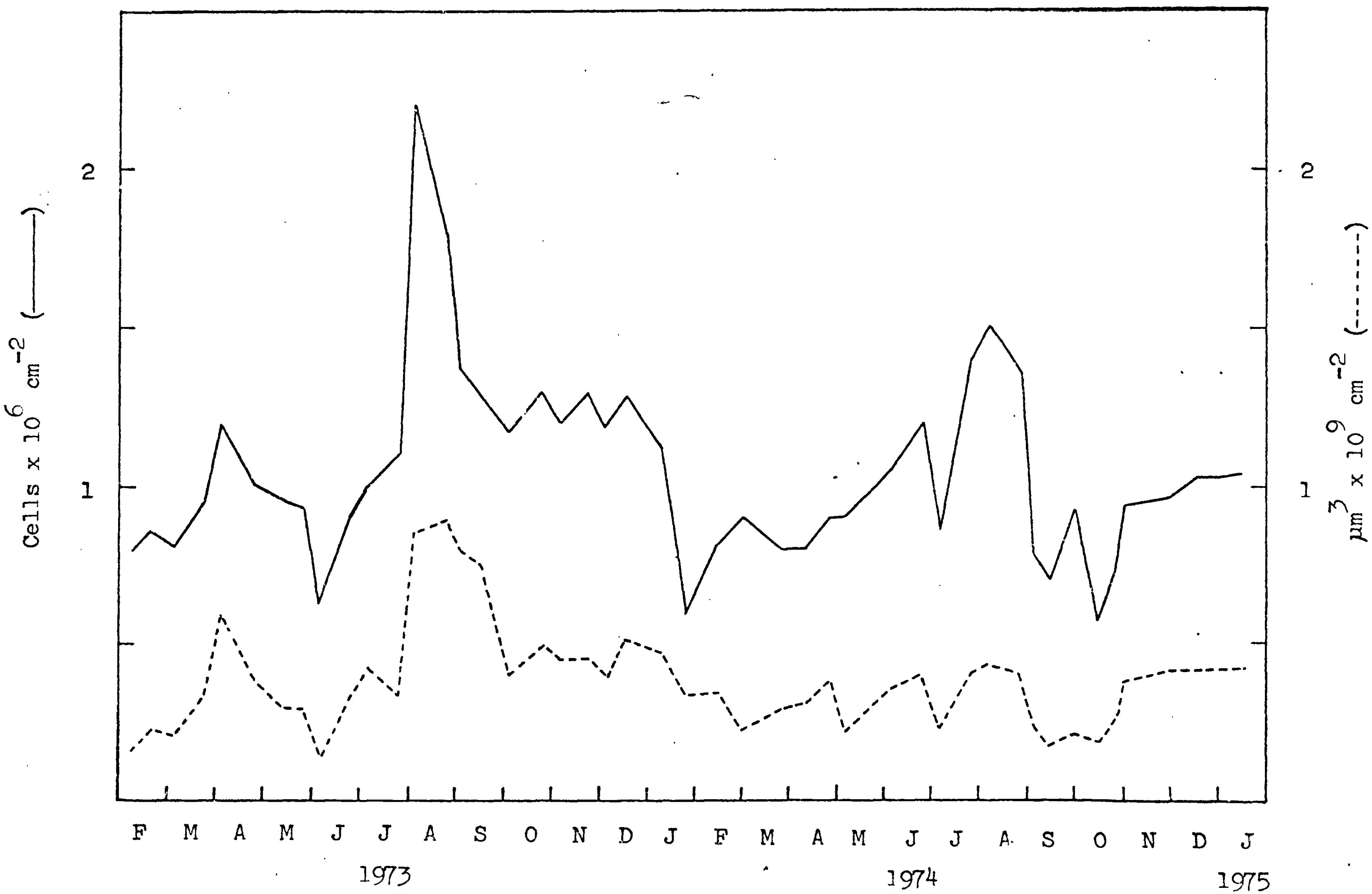

Fig. 39. Seasonal changes in the standing crop of the entire algal assemblage epiphytic upon water cress in the Kennett and Avon Canal.

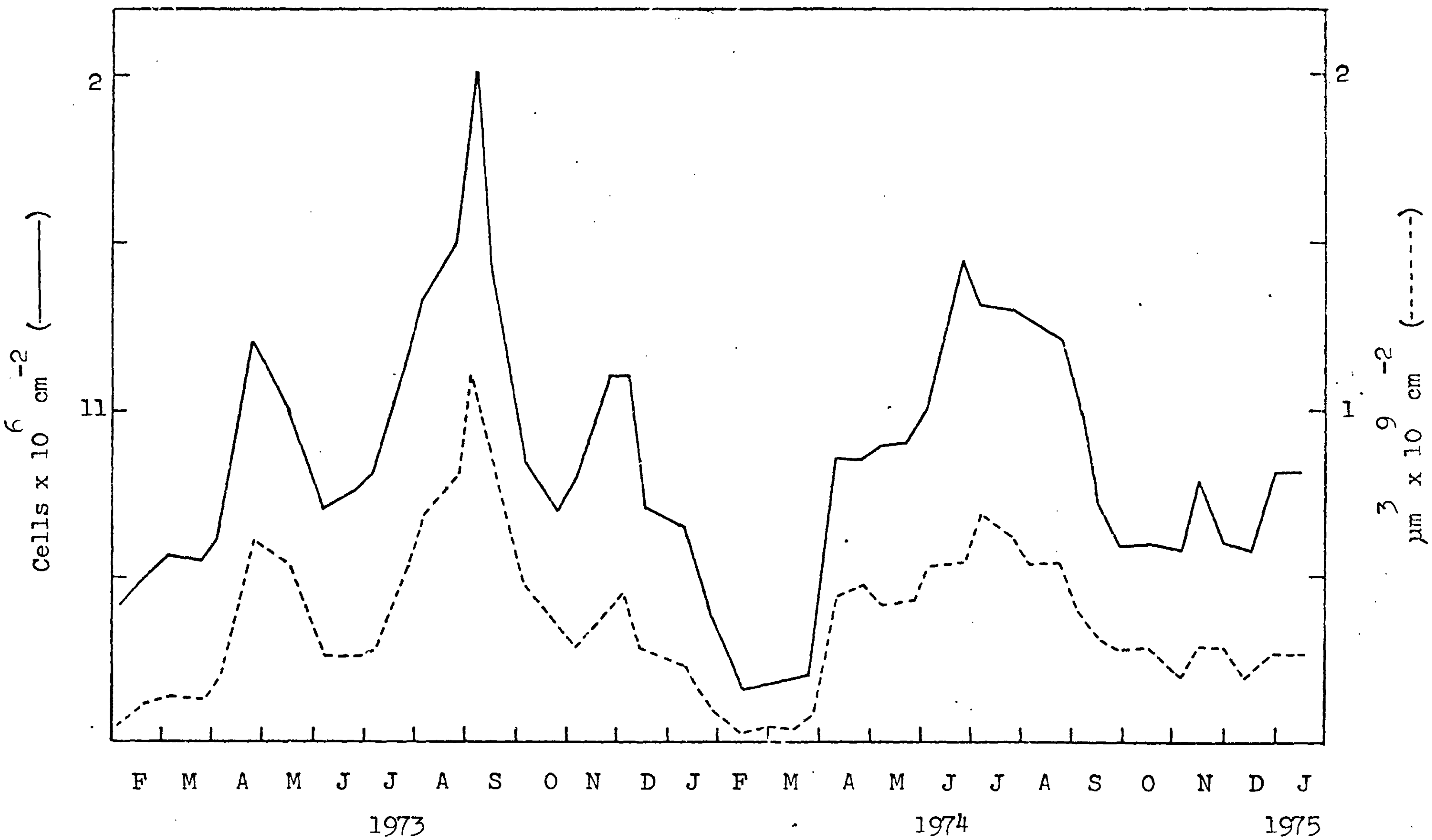

Fig. 40. Seasonal changes in the standing crop of the entire algal assemblage epiphytic upon pond weed in the Kennett and Avon Canal.

Discussion

The low standing crop of phytoplankton in the canal where higher plants and Cladophora were abundant, parallel similar correlations found in other studies (e.g. Hasler and Jones, 1949). Fitzgerald (1969) has suggested that the basis of this apparent "antagonism" is due to competition for limiting supplies of nitrogen. In the present study, however, since nitrates as well as phosphates always occurred in relatively large concentrations, some other environmental parameter had apparently restricted growth. Whatever this factor was, it failed to limit the epiphyte population, a surprising feature considering Fitzgerald (1969) noted that macrophytes also normally have an "antagonistic" effect towards the algae that are attached to higher plants.

The significant development of Trachelomonas volvocina v. minuta in April 1974 follows the pattern of growth of this species noted several years earlier in a nearby pond (Hickman, 1974a). Water temperatures in both areas averaged 12°C at this time suggesting that this factor might have been influencing development. This view is supported by the fact that in the canal during the spring of the previous year, when water temperatures were consistently lower, the period of increased growth exhibited by the population was delayed by several weeks. Chlamydomonas monadina maintained comparatively large numbers throughout the study, as it also did in the Avon and in the previously mentioned pond (Hickman, 1974a).

The standing crop of the epiphytes associated with Cladophora showed considerably greater seasonal variation than those attached to Nasturtium and Groenlandia. This feature is probably due to the fact that virtually the whole of the surface area of these latter two genera was occupied with algae throughout the investigation, thereby limiting the number of attachment sites available for further colonization. Gomphonema spp., whose highest standing crops occurred in the summer, is, however, a species which, through the formation of stalks, can support a high density on a much smaller area of the substrate than is normal among many epiphytes. Despite the high degree of colonization on Nasturtium and Groenlandia, the standing crop of the epiphytes showed no massive decline after reaching its peak in the summer as is normally the case in epipelic and epilithic communities unless there is a prior period of flooding. This may be connected with the fact that a relatively high density of epiphytes occurs on the oldest leaves of several different species of higher plants (Godward, 1934), which suggests that at the end of the growing season the substrate provided by the plant has not undergone a marked deterioration.

Although the algal communities on Cladophora began to expand at the same time during the spring of both years, considerable variability existed in the pattern of change during the following summer. While water velocity plays a key role in determining the ultimate size of the epiphyte populations developed on Cladophora (page 61), this parameter remained comparatively stable in the canal. The only plausible explanation at present for the differential growth patterns is that because of the limited pool of epiphytic taxa, small changes in environmental conditions may produce a greater effect on the total standing crop of these algae than in communities where a greater variety of forms are present.

One of the most striking features of this investigation is the high numbers of Achnanthes minutissima v. cryptocephala maintained on all three plants throughout the year, a pattern also observed in the Wylye and by Douglas (1958) and Dillard (1969) for other areas. Since Achnanthes minutissima is, when it occurs as an epiphyte, normally rare in both fast flowing and still water (Godward, 1934; Whitton, 1970), the rate of water flow is clearly of great importance in governing its distribution. However, in other habitats (rocks and sediments), water flow appears to be of less significance (cf. Douglas, 1958; Stockner and Armstrong, 1971; Moore, 1972) as it is also, but to a lesser extent, in other epiphytic diatoms (Whitton, 1970). Although the similarity in the relative abundance of Achnanthes minutissima on the three plants might be regarded as surprising in view of the differences in the nature of the three substrates, this diatom is very abundant and widespread throughout the northern temperate zone(Jones, 1949, 1951; Sherman and Phinney, 1971) indicating considerable adaptability to different substrate types. It is also important to note that considerable homogeneity in the species composition of the epiphytes associated with several different species of higher plants has been noted by Godward (1934). The rapid growth of Achnanthes during the summer is consistent with the data of Besch et al. (1970) and Moore (1972) for epilithic and epipelic communities.

Although a large number of isopods (Asellus aquaticus) and amphipods (Gammarus pulex) occurred among the growths of Cladophora and both contained a considerable amount of algae in their gut, it seems unlikely that their grazing could cause significant depletion of the epiphyte population (see page 85). Large quantities of algae were also found in the gut of clams (Pisidium sp.), but the density of these animals was always relatively low.

Wellow Brook

Wellow Brook measures approximately 20 km in length, falling about 130 m to its juncture with the Avon River. It flows mainly through pasture but several population centres are situated on its banks. In the vicinity of the collection sites (Lat. 51° 18'; Long. 2° 24'), all of which were unshaded, the river was 10 m in width and much of its bed was covered with growths of Cladophora glomerata. Samples of both epipelic and epilithic algae were taken from sites located 0.5 - 1.0 m from the shore, while collections of the epiphytes associated with Cladophora were made in four areas with different average current velocities, i.e. 10 - 25, 26 - 45, 46 - 65, 66 - 85 cm sec^{-1}.

Physico - chemical Analyses

Water temperatures in Wellow Brook averaged 11.5°C in June 1973 rising to 15.5°C in August but then falling again to 4.5°C by March 1974 (Fig. 41). Values subsequently increased to 17.5°C during the following summer decreasing to about 7°C in the winter. Both water velocity and depth over the epipelic and epilithic collection sites fluctuated a great deal during the study with minimum and maximum values of 2.5 and 69 cm sec^{-1} and 4 and 35 cm respectively (Fig. 41). Changes in water flow over the four different epiphytic sites paralleled those described for the other collection areas but the range in values, discussed later, was relatively small. The pH of the water remained high, ranging from 7.3 to 8.3, and nutrients were always abundant (Table 20). The organic content of the sediment fluctuated between 5 and 8% of the total dry weight.

Epipelic Communities

The epipelic community in Wellow Brook was restricted compared to similar assemblages in the other rivers under investigation. Only 150 different species and varieties were recorded, of which 139 belonged to the Bacillariophyta, ten to the Chlorophyta and nine to the Cyanophyta. The most common species were Surirella ovata v. minuta, Navicula viridula v. minor and Cocconeis placentula v. euglypta while the predominant cyanophytes and chlorophytes were Phormidium sp., Oscillatoria brevis and Scenedesmus spp. (Fig. 42, Table 21). Surirella

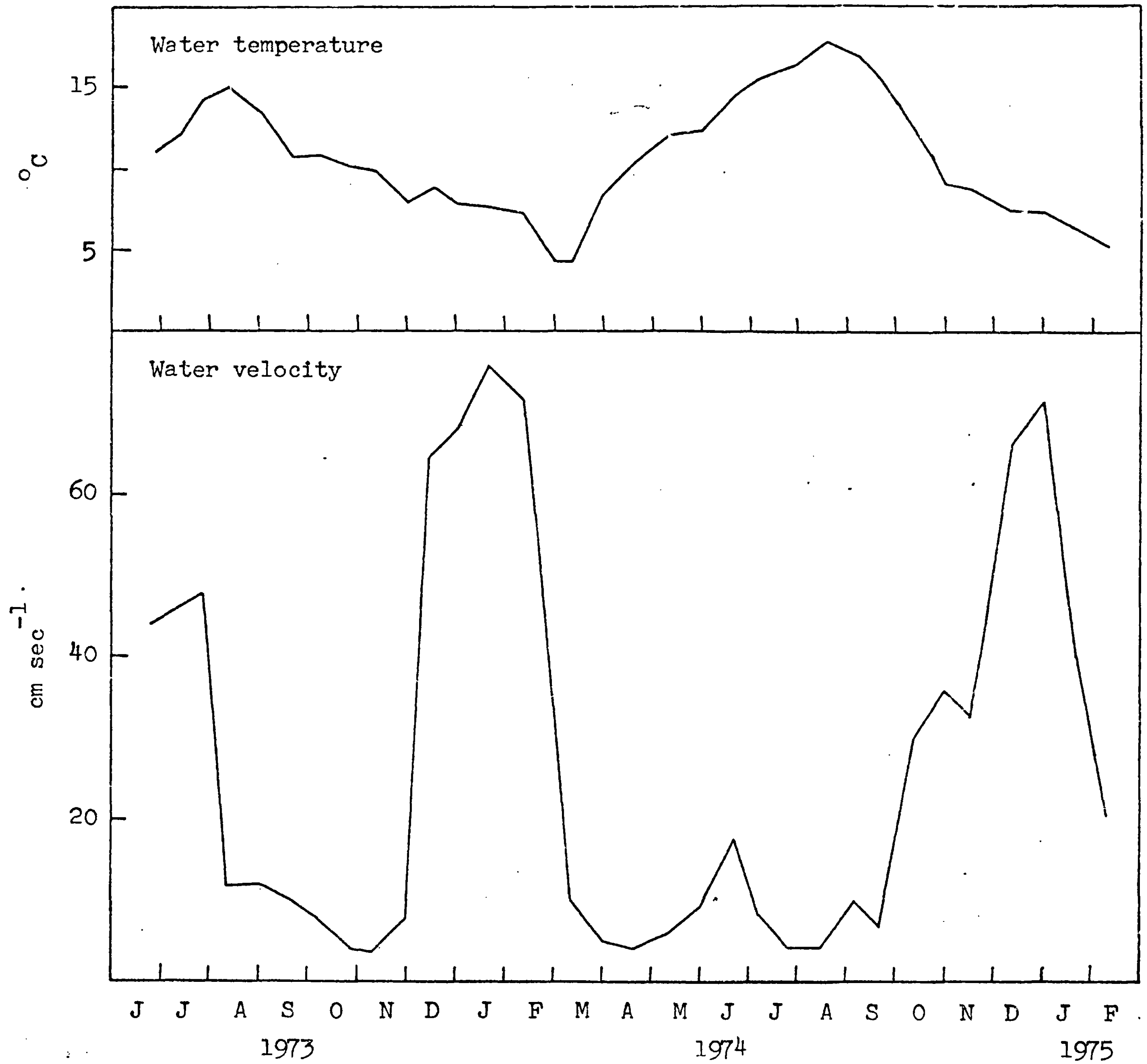

Fig. 41. Seasonal changes in the temperature of Wellow Brook together with the water velocity over the epipelic collection sites.

Table 20. Physico-chemical properties of water from Wellow Brook during 1973 and 1974. Except for pH, all data are expressed in terms of mg l^{-1}.

Parameter	Average	Range
pH	8.0	7.3 - 8.3
Total Alkalinity	349	260 - 390
Silica	6.3	4.1 - 11.5
Orthophosphate-Phosphorus	0.1	0.05 - 0.7
Nitrate-Nitrogen	3.9	2.5 - 6.1

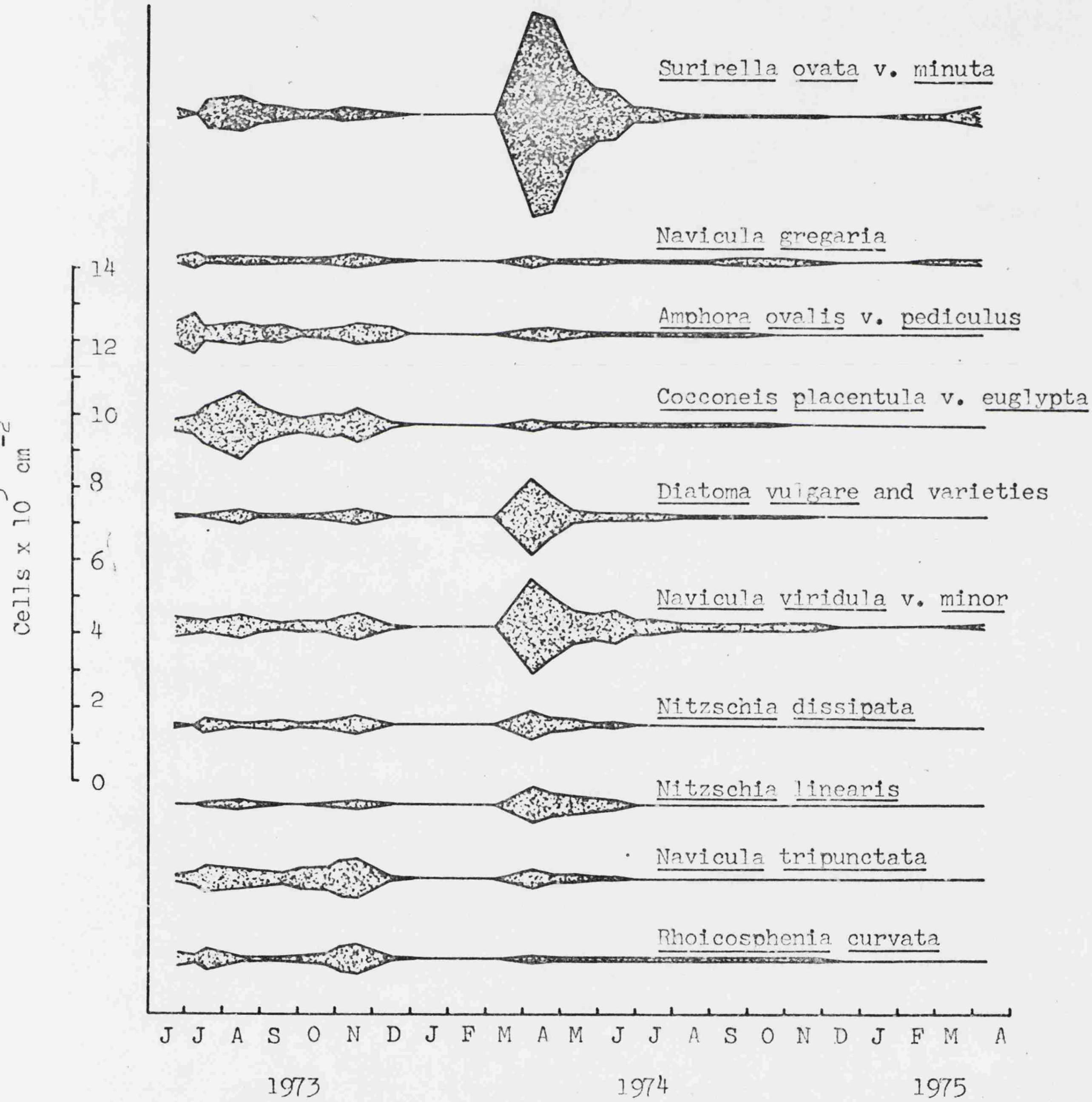

Fig. 42. Seasonal changes in the standing crop of common epipelic algae in Wellow Brook.

Table 21. List of epipelic algae collected from Wellow Brook which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes minutissima v. *cryptocephala*

Amphora ovalis v. *pediculus*

Cocconeis placentula v. *euglypta*

Diatoma vulgare

Fragilaria intermedia

Navicula gregaria

Navicula minima

Navicula tripunctata

Navicula viridula

Nitzschia apiculata

Nitzschia dissipata

Nitzschia linearis

Rhoicosphenia curvata

Surirella ovata v. *minuta*

Phormidium sp.

exhibited a well defined spring bloom during March and April of both 1974 and 1975 when densities of up to 5.6×10^5 cells cm^{-2} were recorded, a pattern also exhibited, but to a lesser degree, by Navicula viridula (Fig. 42). Cocconeis placentula, on the other hand, as well as several other less abundant taxa, such as Amphora ovalis v. pediculus, Navicula tripunctata and Rhoicosphenia curvata, although showing considerable development during the warmer months, never exhibited sharp increases during the spring.

The total standing crop of the flora remained relatively constant during the summer of 1973 but rose sharply to 1.3×10^6 cells cm^{-2} (1.5×10^9 μm^3 cm^{-2}) in November, only to fall to insignificant levels during the winter (Fig. 43). A well defined spring bloom began during March 1974 with peak values,(1.5×10^6 cells cm^{-2}; 2.0×10^9 μm^3 cm^{-2}) being recorded in April. Thereafter, the standing crop fell sharply and low levels were maintained throughout the summer and following winter.

The fastest daily rates of recruitment into the community occurred during November 1973 when values of up to 7.3×10^4 cells cm^{-2} and 8.3×10^7 μm^3 cm^{-2} were recorded followed by March 1974 with values of 5.0×10^4 cells cm^{-2} and 8.2×10^7 μm^3 cm^{-2} (Fig. 43). The most rapid daily rate of disappearance of algae from the sediments, 4.0×10^4 cells cm^{-2} and 5.7×10^7 μm^3 cm^{-2}, occurred during December 1973 but nearly comparable values were recorded in May 1973.

Epilithic Communities

The diversity of the epilithic community in Wellow Brook was similar to that of the epipelic assemblage with 125 diatoms, nine chlorophytes and 11 cyanophytes being identified. The predominant species in the first group of algae were Navicula viridula v. minor, N. tripunctata and Surirella ovata v. minuta while Scenedesmus dimorphus, Oscillatoria brevis and Phormidium foveolarum were the most common members of the other groups (Table 22 , Fig. 44). As in the epipelic community, both Surirella and N. viridula v. minor exhibited a spring bloom in numbers during both 1974 and 1975, while in the case of several other taxa e.g. Amphora ovalis v. pediculus, Diatoma vulgare, Navicula tripunctata, Nitzschia dissipata and Phormidium foveolarum,

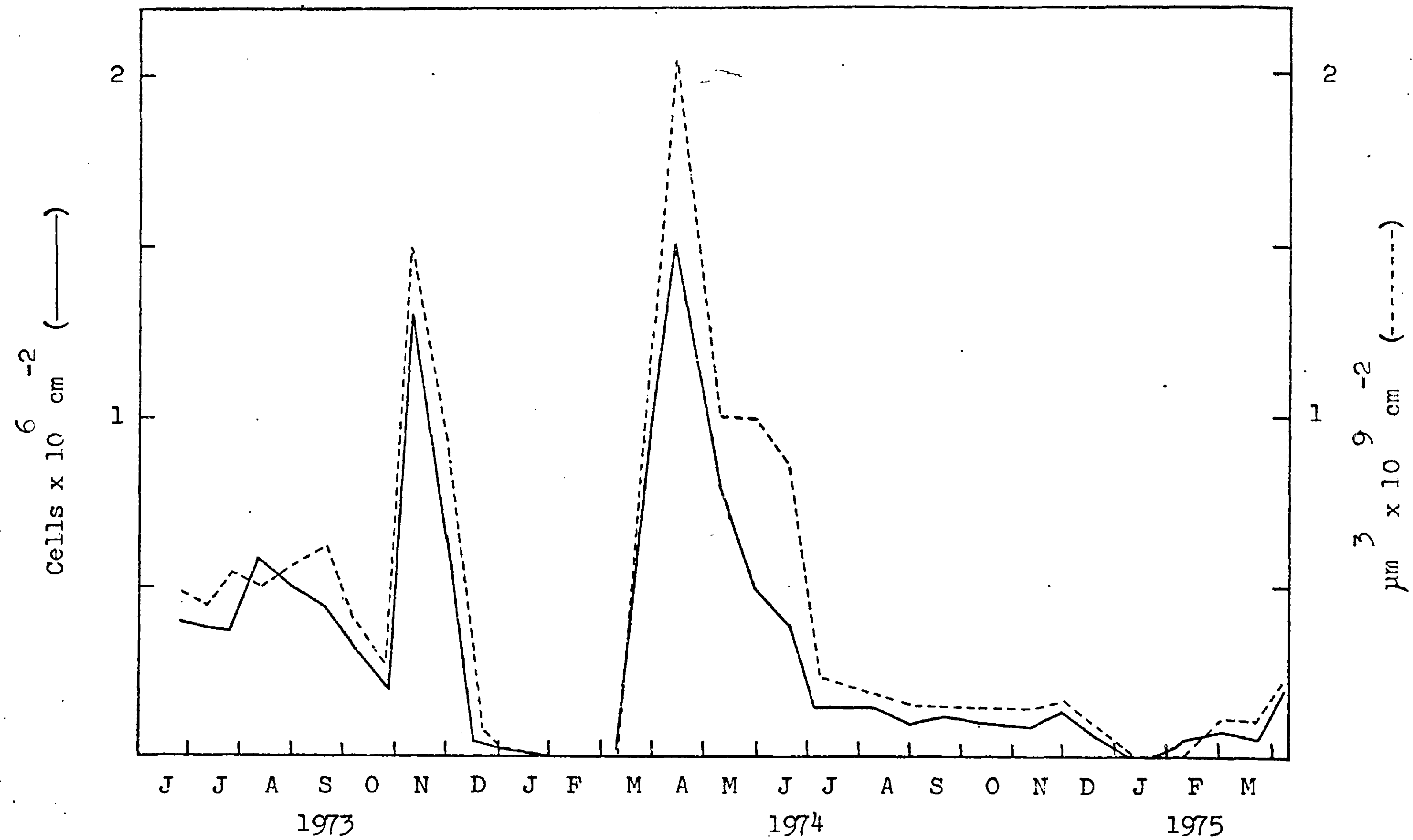

Fig. 43. Seasonal changes in the standing crop of the entire epipelic assemblage in Wellow Brook.

Table 22. List of epilithic algae collected from Wellow Brook which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Amphora ovalis v. *pediculus*
Cocconeis placentula v. *euglypta*
Diatoma vulgare
Diatoma vulgare v. *breve*
Gyrosigma spencerii
Navicula cryptocephala v. *veneta*
Navicula gregaria
Navicula krasskei
Navicula tripunctata
Navicula viridula v. *minor*
Nitzschia acicularis
Nitzschia dissipata
Nitzschia linearis
Nitzschia palea
Rhoicosphenia curvata
Surirella ovata v. *minuta*
Oscillatoria brevis

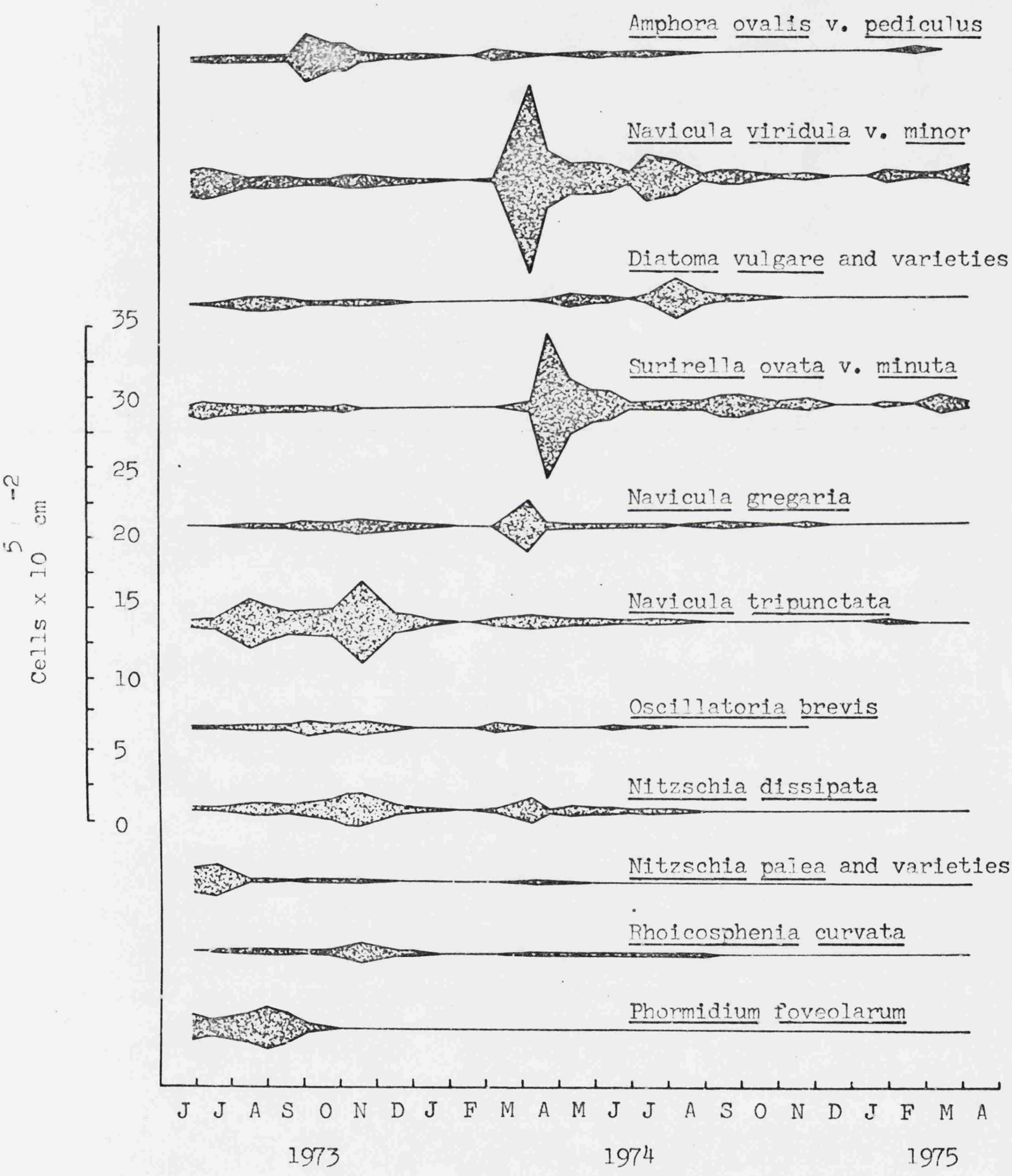

Fig. 44. Seasonal changes in the standing crop of common epilithic algae in Wellow Brook.

this pattern of growth was not found. The standing crop of the entire assemblage remained high, 1.2 - 1.7 x 10^6 cells cm^{-2}, 1.2 - 2.2 x 10^9 μm^3 cm^{-2}, during the summer and autumn of 1973 but fell to insignificant levels by February 1974 (Fig. 45). A well defined spring bloom occurred towards the end of March with values decreasing more or less uniformly through the summer and autumn. During the first three months of 1975 the standing crop of the flora remained at comparatively low levels.

The fastest daily growth rates occurred during the spring bloom in 1974 when values of 7 x 10^4 cells and 7 x 10^7 μm^3 cm^{-2} were recorded. Algae disappeared most quickly from the rocks during December 1973 (8 x 10^4 cells and 4.7 x 10^7 μm^3 cm^{-2}) but high rates, i.e. 4.3 x 10^4 cells and 4.5 x 10^7 μm^3 respectively, also occurred in April 1974.

Potamoplankton and the Planktonic Communities

The planktonic community in Wellow Brook consisted of 28 species of which 12 belonged to the Chlorophyta, seven to the Euglenophyta, five to the Cyanophyta and two to the Bacillariophyta and to the Chrysophyta (Table 23). The predominant species, Chlamydomonas monadina, showed maximum development between June and October when it accounted for up to 20% by numbers of all the algae floating in the stream. Crucegenia tetrapedia, on the other hand, was observed in large numbers during September 1973 (20%) rising to dominance (50 - 60%) in October and November but thereafter it occurred only in small densities. The predominant euglenoids and cyanophytes, Merismopedia punctata, M. tenuissima and Trachelomonas volvocina v. minuta occurred most abundantly during the summer of both years but seldom represented more than 1 - 2% of the flora. As with the other study rivers, the potamoplankton was well developed with 187 different kinds of diatoms being recorded (Table 23). The standing crop of the entire assemblage in Wellow Brook remained relatively low throughout the study (Fig. 46). The highest values, which never exceeded 4.2 x x 10^5 cells l^{-1} (4.2 x 10^8 μm^3 l^{-1}), occurred during the summer of both 1973 and 1974 while in the winter few if any algal cells were found in the water.

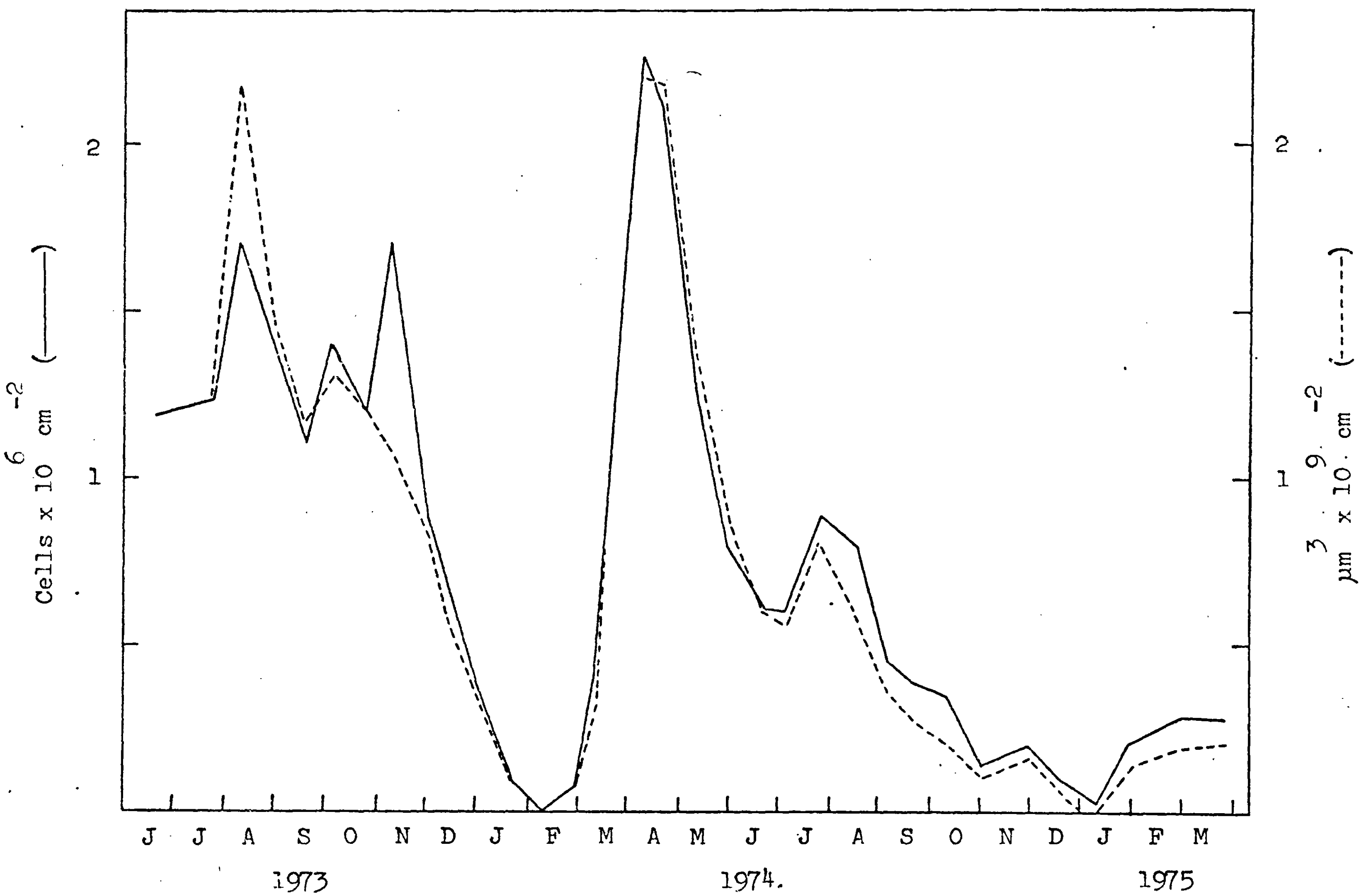

Fig. 45. Seasonal changes in the standing crop of the entire epilithic assemblage in Wellow Brook.

Table 23a. List of algae floating in Wellow Brook which accounted for more than 10% of the flora on at least one sampling date.

Achnanthes lanceolata
Achnanthes minutissima v. *cryptocephala*
Cocconeis pediculus
Cocconeis placentula v. *euglypta*
Diatoma vulgare
Navicula viridula v. *minor*
Nitzschia acicularis
Nitzschia linearis
Nitzschia palea
Rhoicosphenia curvata
Chlamydomonas monadina
Crucegenia tetrapedia

Table 23b. List of planktonic algae collected from Wellow Brook which accounted for between 1 and 10% of the flora on at least one sampling date.

Cyclotella comta
Ankistrodesmus falcatus
Chlamydomonas sp.
Scenedesmus dimorphus
Scenedesmus quadricauda
Oocystis sp.

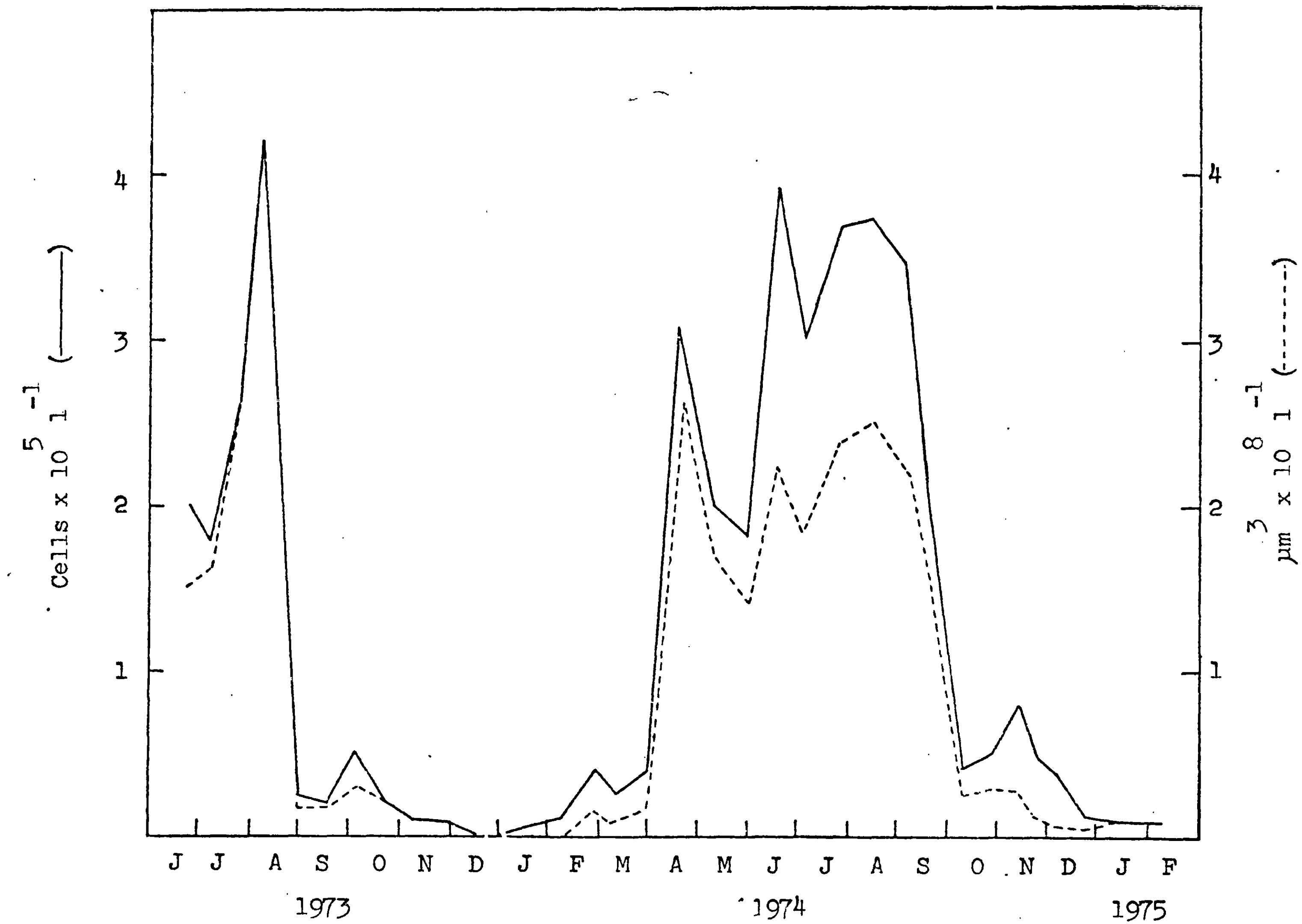

Fig. 46. Seasonal changes in the standing crop of the entire algal assemblage floating in Wellow Brook.

Epiphytic Communities

During most of the investigation, the current velocity of the four epiphytic collection areas fell within the average range described earlier, i.e. 10 - 25, 26 - 45, 46 - 65 and 66 - 85 cm sec^{-1}. However, during periods of extremely high water, i.e. December and January, the current velocity in all areas exceeded 45 cm sec^{-1} and, on occasion, reached 100 cm sec^{-1}. The total standing crop of Cladophora in water flowing at 10 - 45 cm sec^{-1} decreased during the summer of 1973 to 1.0 g m^{-2} but increased to 1.5 g m^{-2} by September only to fall again to low overwintering levels by the first of November (Fig. 47). A gradual increase in the amount of this alga began in March peaking at a value of 1.05 g m^{-2} in September before decreasing to insignificant levels by January 1975. The standing crop of Cladophora in the faster flowing areas was not determined.

The entire epiphytic community associated with Cladophora glomerata in Wellow Brook was represented by 183 different kinds of algae, of which 160 were members of the Bacillariophyta while the corresponding values for the Cyanophyta, Chlorophyta and Euglenophyta were 13, nine and one respectively. The predominant species in the first group of algae were Rhoicosphenia curvata, Cocconeis pediculus, C. placentula v. euglypta and Navicula viridula v. minor while Chamaesiphon incrustans and Lyngbya spp. were the predominant cyanophytes.

In the rapid water collection area (greater than 65 cm sec^{-1}), Rhoicosphenia curvata was invariably predominant, normally accounting for 60 - 90% by numbers of the flora. Cocconeis placentula v. euglypta was usually second in importance representing up to 18% of the assemblage during June and July of both 1973 and 1974. Most other species occurred only in small numbers throughout the investigation but during April and May 1974, Diatoma vulgare attained considerable importance, i.e. 30 - 35%.

In the medium fast collection area (46 - 65 cm sec^{-1}), R. curvata retained dominance representing on the average 58% by numbers of the total algal assemblage. Although the abundance of this species fluctuated a great deal during the investigation (24 - 84%), no distinct pattern of change was in evidence. The fall in abundance of R. curvata was matched by a corresponding rise in the numbers of C. placentula v.

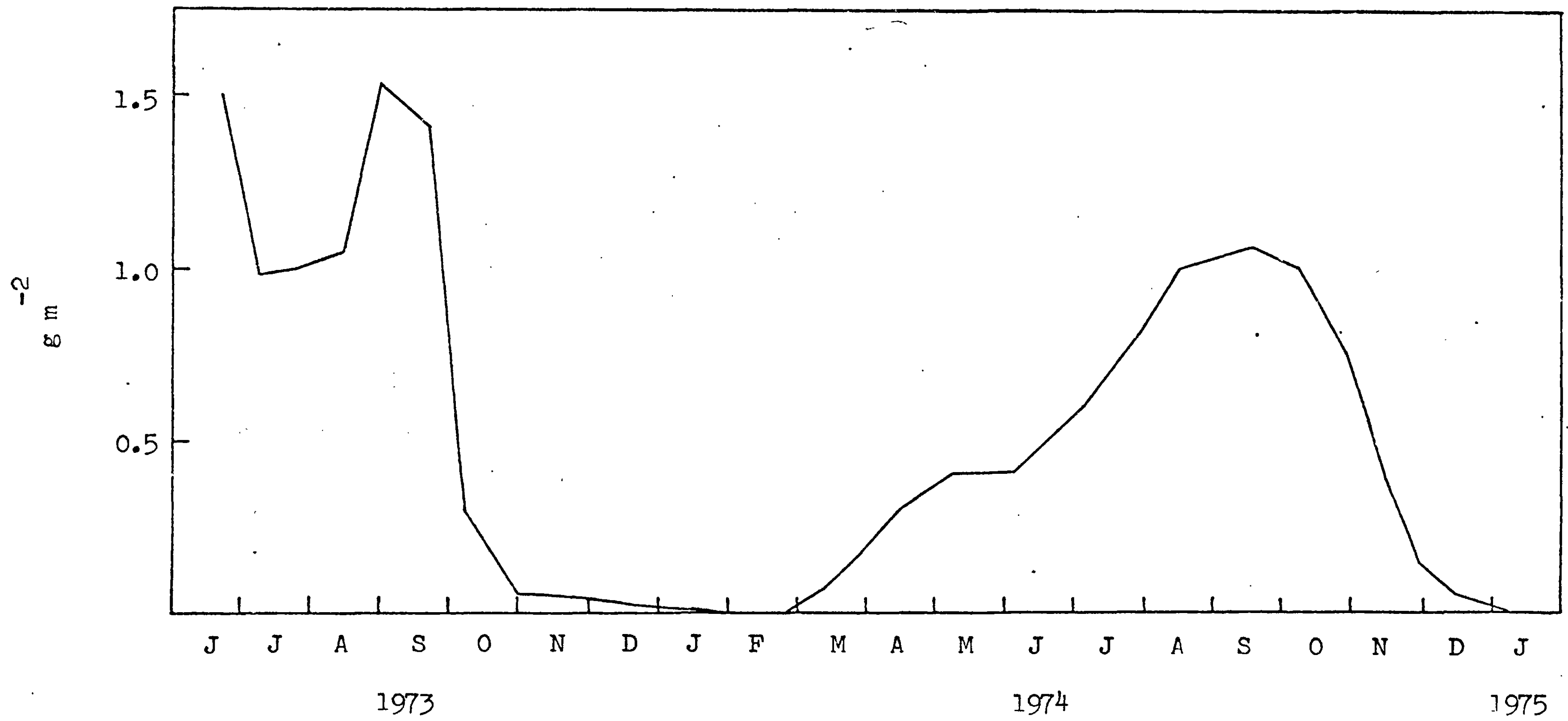

Fig. 47. Seasonal changes in the dry weight of <u>Cladophora glomerata</u> attached to rocks in Wellow Brook where the water flowed at 10-45 cm sec^{-1}.

euglypta, which during July and August represented from 20 to 33% of the flora. As in the rapid water collection area, D. vulgare attained importance (22 - 32%) during April and May 1974, a pattern also exhibited by Navicula viridula (27 - 30%).

The above trends were even more exaggerated in the medium slow collection area (28 - 45 cm sec^{-1}) with R. curvata representing, on the average, only 45% of the total algal assemblage (range 26 - 74%). Although C. placentula v. euglypta exhibited a sharp increase in importance, accounting for 42 - 51% of the assemblage during July and August of both 1973 and 1974, the most dramatic shift was in the appearance of Cocconeis pediculus. This taxon, although rare throughout most of the year, accounted for 18 - 30% of the assemblage between the months of October and January. As in the other collection areas, both D. vulgare and N. viridula exhibited considerable development (40 and 52% respectively) during the spring of 1974 and it is also important to note the appearance for the first time of Chamaesiphon incrustans (2 - 4%) during the summer and autumn of 1973.

Rhoicosphenia curvata accounted for an average of only 35% of the epiphytes growing in Wellow Brook where the water normally flowed slower than 25 cm sec^{-1}. Several distinct peaks in the relative abundance of this species were noted and occurred immediately after periods of high water when the current exceeded 25 cm sec^{-1}. Cocconeis placentula v. euglypta showed improved development compared with the faster flowing areas, representing from 35 to 42% of the flora during the autumn of 1973 and from 20 to 42% between June and December 1974. Cocconeis pediculus also increased in importance, accounting for 20 - 30% of the total assemblage during the autumn and winter of both years. This general trend was also exhibited by Diatoma vulgare, Navicula viridula v. minor and especially Chamaesiphon incrustans for which values of between 30 and 47% were recorded during the autumn and winter of 1973.

Seasonal changes in the absolute abundance of Rhoicosphenia curvata growing in relatively fast water, i.e. greater than 65 cm sec^{-1}, were characterized by a well defined bloom (3.9×10^{6} cells g^{-1}) in the spring with relatively high numbers being maintained throughout most of the investigation (Fig. 48). Navicula viridula and Diatoma vulgare,

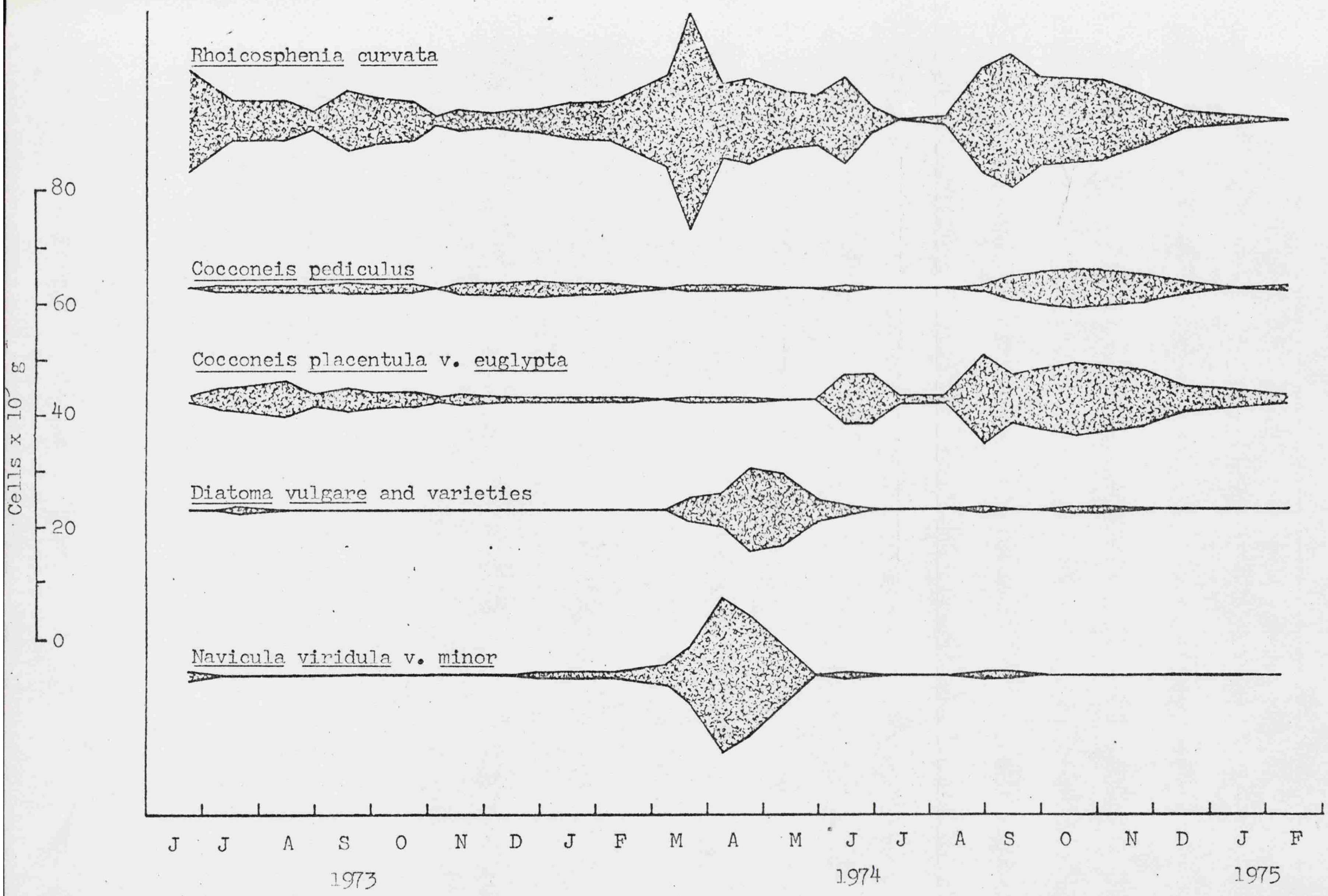

Fig. 48. Seasonal changes in the standing crop of common algae epiphytic upon *Cladophora glomerata* in Wellow Brook where the water flowed faster than 65 cm sec^{-1}.

on the other hand, normally occurred in only small numbers but in April 1974 respective values of 2.8×10^6 and 1.5×10^6 cells g^{-1} were recorded. Both Cocconeis pediculus and C. placentula v. euglypta failed to show a distinct increase in numbers throughout the investigation. Although the seasonal abundance of the predominant species in the medium fast collection area almost exactly paralleled that outlined above, the density of the flora in the slower reaches of Wellow Brook differed considerably from the rapid water collection area (Fig. 49). Thus, R. curvata attained a maximum density of 4.6×10^7 cells g^{-1} and C. pediculus and C. placentula v. euglypta, which showed distinct blooms in the autumn of both years contrasting with the rapid water collection site, maintained populations of up to 4.2×10^7 and 3.2×10^7 cells g^{-1}. Similarly, although Chamaesiphon incrustans occurred in only small numbers in 1974, densities of up to 1.9×10^7 cells g^{-1} were observed during the autumn and winter of 1973.

The total standing crop of the epiphytes growing in fast flowing water (i.e. greater than 65 cm sec^{-1}) remained low throughout 1973 but increased sharply during March and April 1974 to 5.9×10^6 cells g^{-1} (5.0×10^9 μm^3 g^{-1}) (Fig. 50). Thereafter, the values decreased irregularly to only 0.4×10^6 cells g^{-1} (0.3×10^9 μm^3 g^{-1}) in August but exhibited considerable recovery during the autumn before declining again. Seasonal changes in the standing crop of the epiphytes in the medium fast collection area almost exactly paralleled those outlined above but this was not the case for the slower flowing reaches of Wellow Brook (Fig. 51). In these areas, the density of the flora, although remaining low during the summer of 1973, increased sharply in September to over 100×10^6 cells g^{-1} before falling to comparatively restricted levels (e.g. 20×10^6 cells g^{-1}) in the winter. The spring bloom in 1974 occurred in February and March with values decreasing considerably in the summer and then rising again in the autumn.

The amount of debris which had settled on the Cladophora, determined by washing the filaments lightly with distilled water and drying the dislodged material by sublimation, increased inversely with water velocity (Fig. 52). Thus, in the fastest flowing areas of Wellow Brook, values seldom exceeded 0.02 g g^{-1} dry weight of Cladophora while, in the relatively calm reaches, weights of up to 2 g g^{-1} were recorded.

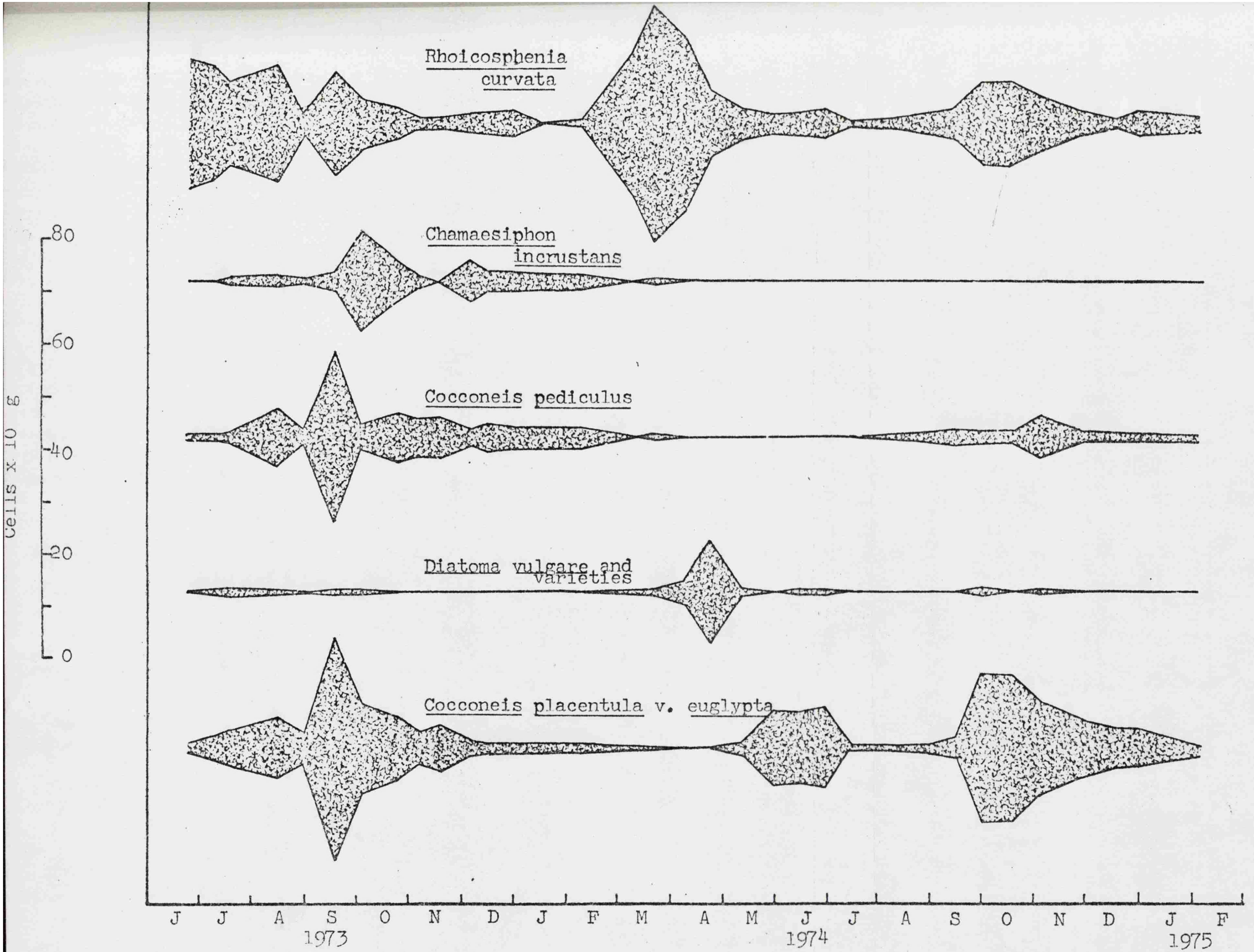

Fig.49. Seasonal changes in the standing crop of common algae epiphytic upon Cladophora glomerata in Wellow Brook where the water flowed at 10-45 cm sec^{-1}.

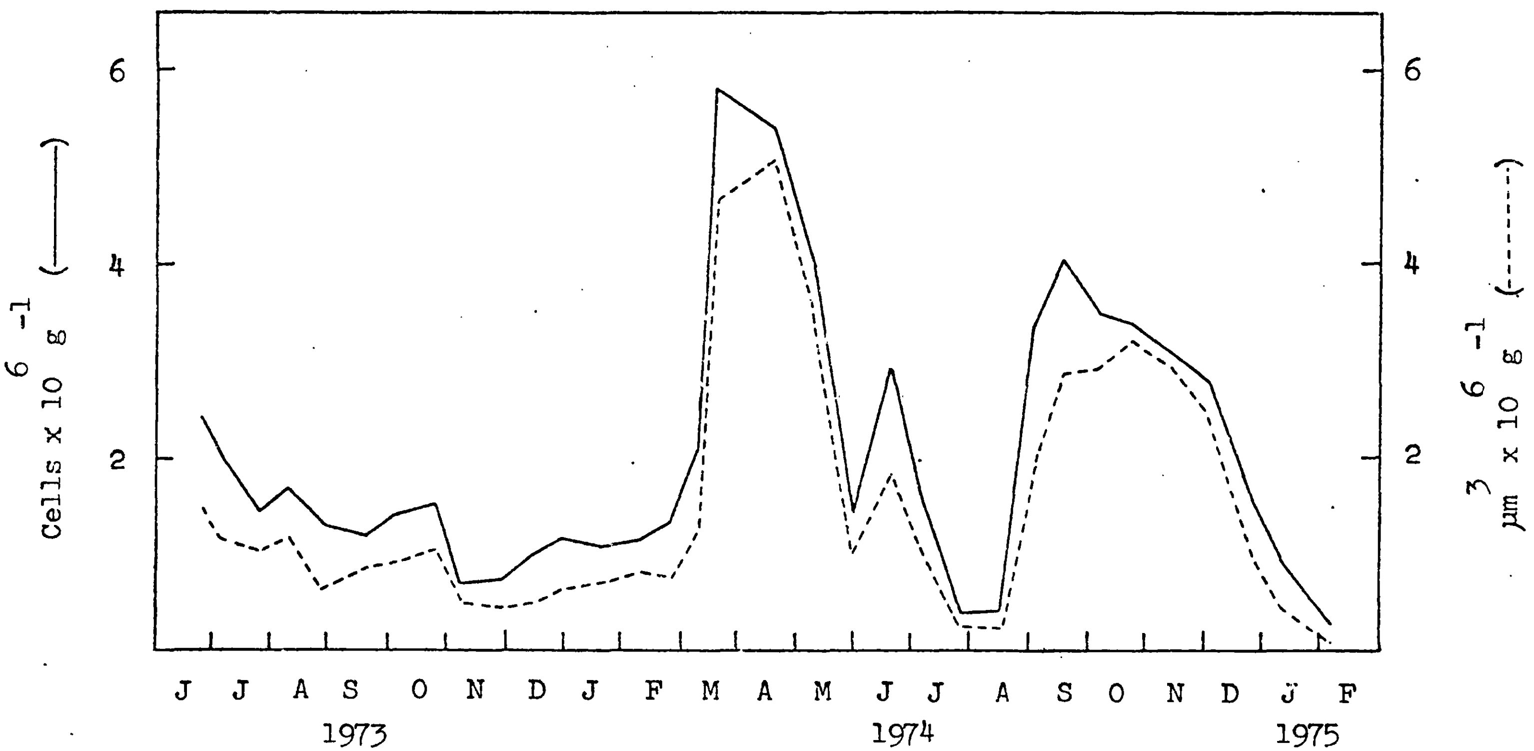

Fig. 50. Seasonal changes in the standing crop of the entire algal assemblage epiphytic upon *Cladophora glomerata* in Wellow Brook where the water flowed faster than 65 cm sec^{-1}.

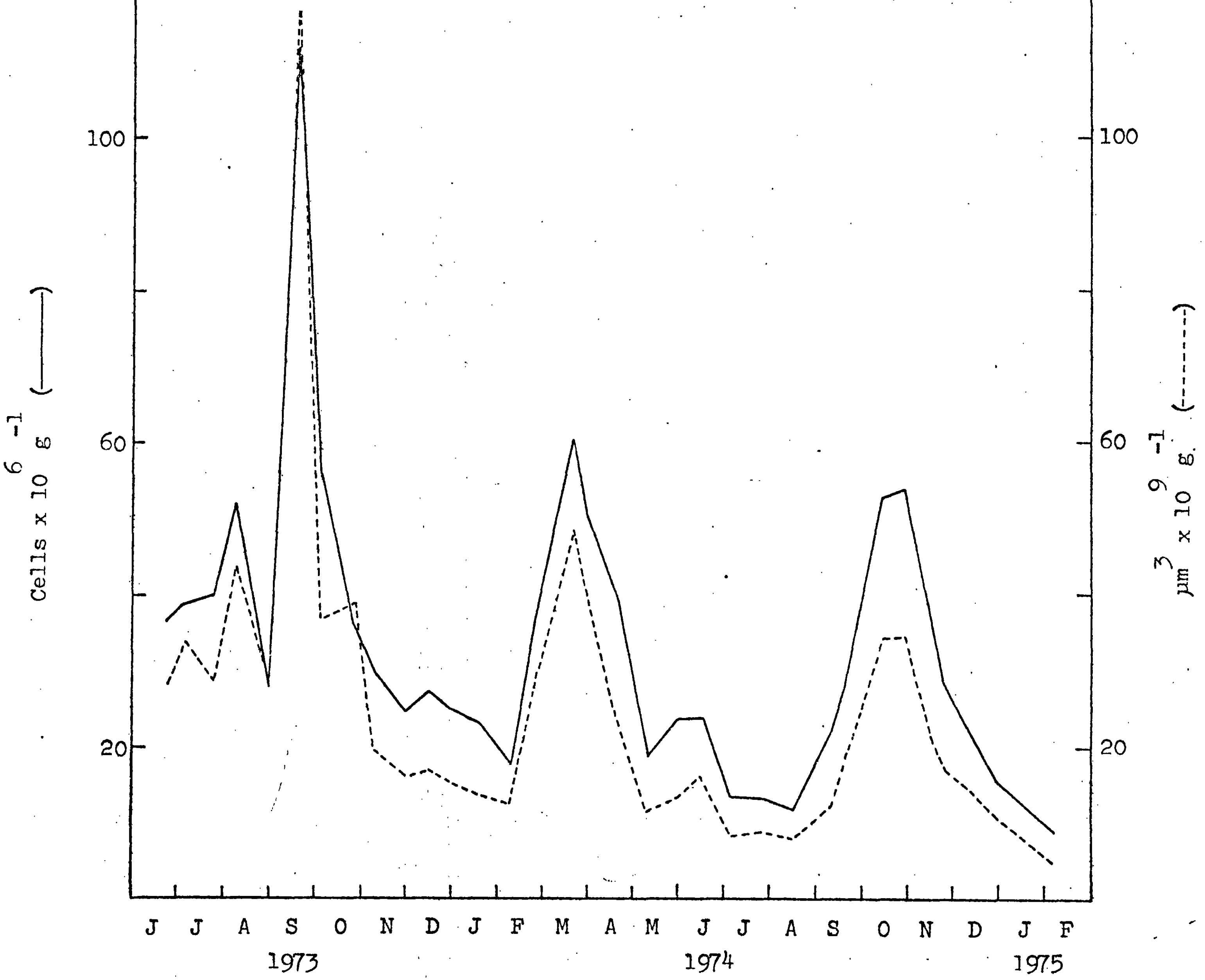

Fig. 51. Seasonal changes in the standing crop of the entire algal assemblage epiphytic upon Cladophora glomerata in Wellow Brook where the water flowed at 10-45 cm sec^{-1}.

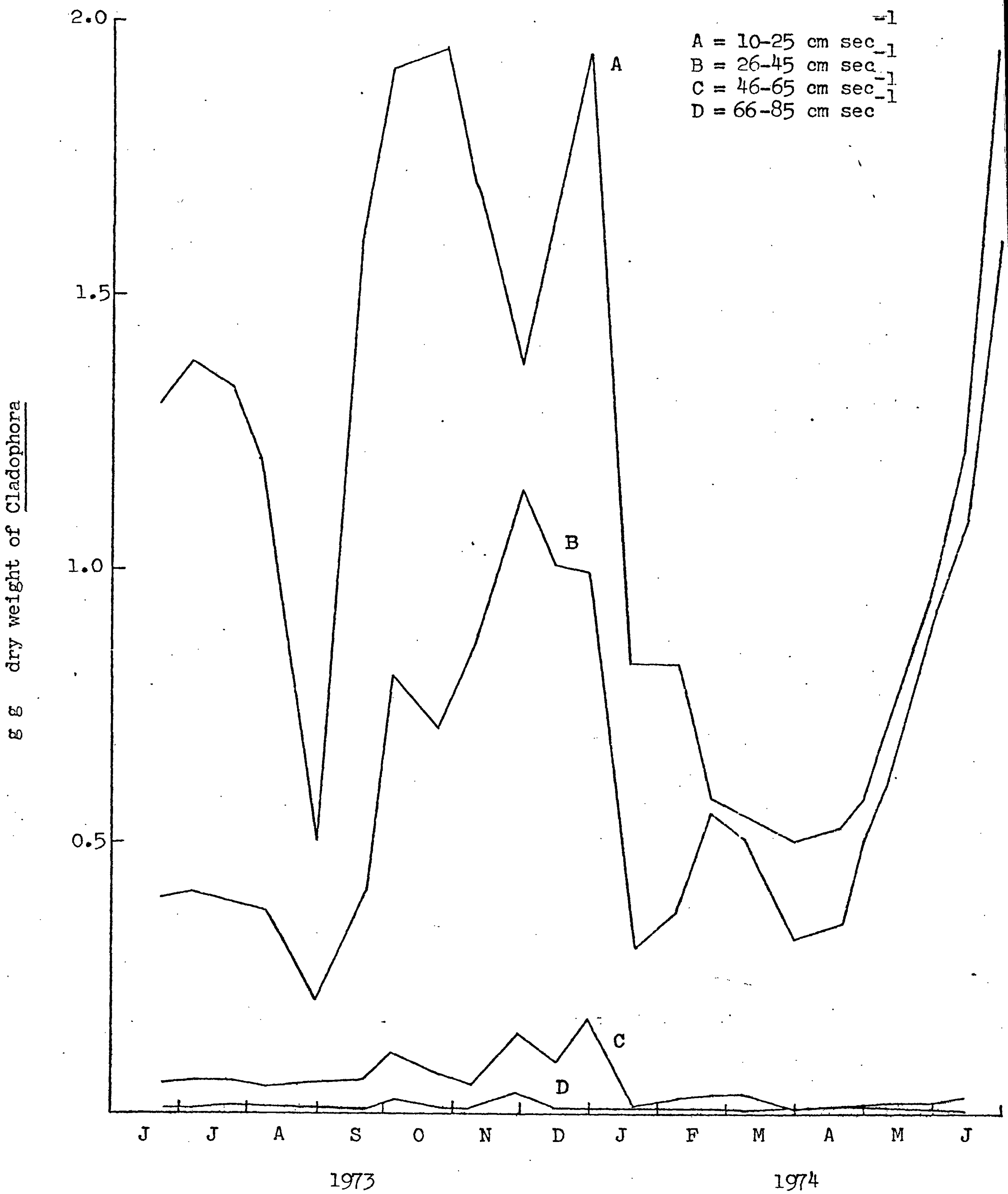

Fig. 52. Seasonal changes in the dry weight of material which had settled on filaments of *Cladophora glomerata* in areas of Wellow Brook with different average water velocity.

Discussion

The relatively low density of both epipelic and epiphytic algae in Wellow Brook during most of the summer, but with a sharp increase in the autumn, is a pattern of growth virtually opposite to that exhibited by *Cladophora*, suggesting that competition for nutrients had limited the standing crop of the microscopic flora during the summer. This view agrees with the data of Fitzgerald (1969) which indicated that higher plants as well as *Cladophora* normally compete more successfully for nutrients than the microflora. Although the pattern of growth exhibited by the epilithic community did not generally follow the above trends, it is important to note that several major differences existed in the species composition of this and the other community.

The decrease in the relative importance of *Rhoicosphenia curvata* and the corresponding rise in *Cocconeis pediculus*, *C. placentula* v. *euglypta* and *Chamaesiphon incrustans* as the rate of water flow decreased, contrasts in many respects with the data of Chudyba (1968). In this latter study, *Cocconeis pediculus* was predominant in fast flowing water while the abundance of *C. placentula* v. *euglypta* remained relatively constant regardless of water velocity. Furthermore, *Rhoicosphenia curvata* showed considerable development at one of the calm sites in Chudyba's study. The reasons for these differences between the two studies are not clearly apparent. It is important to note however that Chudyba sampled over the period of only eight days and the pattern of species distribution did, for short periods in the present investigation, sometimes parallel that described by Chudyba. This was particularly the case after periods of high water when, for example, *Rhoicosphenia curvata* became predominant in the calmer reaches of Wellow Brook.

The maximum development of representatives of *Rhoicosphenia curvata* during the spring parallels the work of Chudyba (1965) and Peabody and Whitton (1968) for other epiphytic populations associated with *Cladophora glomerata*. Similarly the upsurge in the abundance of *Cocconeis* spp. in September was also reported by Eichenberger (1967) but Peabody and Whitton (1968) found that *C. pediculus* was most common in the summer, a feature also noted by Butcher (1940) for *C. placentula*. Both *Diatoma vulgare* and *D. vulgare* v. *producta* bloomed in the spring and, while Chudyba (1968) observed a similar upsurge in the case of the former species, D. vulgare v. producta occurred most abundantly later in the year. The seasonal pattern in the abundance of R. curvata, D. vulgare and Navicula viridula v. minor was similar regardless of ambient water velocity but, in the case of C. placentula v. euglypta, rapidly flowing water suppressed the characteristic autumn bloom. This latter feature may indicate that water flow can significantly effect the rate of cell division in at least certain algal species.

The total standing crop of the epiphytes was much greater in the calmer reaches of Wellow Brook than in torrential areas, a difference which is probably due, at least in part, to detachment, but as mentioned above the rate of cell division may also have been significantly retarded in the torrential area. Very high growth rates occurred during the autumn in all collection areas suggesting that environmental conditions were relatively unfavourable during the spring and summer. Presumably, competition with Cladophora for nutrients at this time, or perhaps the production of growth-inhibiting metabolites by Cladophora, were primarily responsible for the difference in development. Despite severe flooding during the winter of both 1973 and 1974, the standing crop of the epiphytes remained high compared with epipelic and epilithic communities, possibly reflecting the relative force of adhesion exhibited by R. curvata. Although some variation existed, seasonal changes in the density of the epiphytes was positively correlated with the amount of debris which had settled on Cladophora. It therefore seems likely that this factor does not limit algal growth, a view further supported by the fact that at even the highest concentration of debris, numerous attachment sites remained available. The high degree of correlation between the standing crop and the amount of debris suggests that the algae were primarily responsible for trapping the suspended material in the water. In this context, Chandler (1937) suggested that macrophytes, through their filtering action, cause significant depletion of planktonic algae and suspended solids in streams.

Animals containing algae in their gut were generally absent from sediments. During 1974, however, representatives of the protozoan Paramecium sp. contained in their gut an average of eight diatom cells per individual. The density of these animals, determined by volumetric subsampling of a known area of sediment (Moore, 1974a), was estimated at approximately 13,600 individuals cm^{-2}, implying that 1.1×10^5 algal cells cm^{-2} had been ingested. This value represents about 10% of the total standing crop of the epipelic algae at this time. The actual feeding rate of Paramecium was not determined but, if the value of 1 cell $animal^{-1}$ h^{-1} obtained by Goulder (1972) for Loxodes magnus Stokes is applicable to within even an order of magnitude, it is apparent that significant grazing of the epipelic flora had occurred.

The diatom Navicula viridula v. minor accounted for about 50% by numbers of the algae in the gut of Paramecium followed by Surirella ovata v. minuta at 35%. Since this latter species was more abundant in the environment than N. viridula, it would appear that there was some degree of food selection. This feature may be explained by the fact that Surirella is usually well attached to the substrate by means of a gelatinous stalk whereas Navicula possesses a less efficient mechanism for attachment and is thus probably much easier to dislodge and ingest. The possibility cannot be excluded, however, that Navicula may have been originally predominant on the sediments but, through the grazing of Paramecium, was reduced to secondary importance. Goulder (1972) suggested that Loxodes was able to distinguish between species within the chlorophyte genus Scenedesmus. In contrast to the effects of grazing by Paramecium, the large numbers of Asellus aquaticus and Gammarus pulex found among the growths of Cladophora did not significantly reduce the standing crop of the epiphytes on this plant (Section 5).

3. The Relative Organic Component Contributed to Rivers by Algae and Detritus

Introduction

Apart from algae, large quantities of particulate decaying plant and animal matter, i.e. organic detritus, also play an important role in the energy cycle of streams and rivers. For example, filter feeders such as molluscs, simuliids and lamprey larvae, make extensive use of suspended detritus and a vast array of invertebrates, including protozoans, oligochaetes, gastropods, crustaceans and insects, utilize the material associated with rocks and sediments (see Hynes, 1970). Although detritus originates from a large number of sources, the results of Efford (1969) suggested that in an oligotrophic Canadian lake he studied, about 85% of the energy budget was derived from forest debris. Since it is practically impossible to separate algae from detritus (Minshall, 1967), most studies on the role of detritus in the energy cycle of rivers have tended either to ignore the associated algal component or to make estimates in terms of surface area (Egglishaw and Shackley, 1971). In this investigation the organic dry weight of the detritus fraction has been deduced in several rivers by obtaining the total weight of material, both suspended in the water and attached to rocks, and then subtracting the weight of algae present.

Materials and Methods

The total weight of suspended solids in the Avon, the Wylye and one of its tributaries, and the Kennett and Avon Canal was determined from one litre aliquots of the previously mentioned plankton samples (page 5). The occasional macro-invertebrate and leaf and stem fragments taken in the sample were always removed. After the water had been filtered through predried and weighed Sartorius membranes (pore size: 1.2, 0.8 and 0.45 µm), the entire sample was dried by sublimation. The organic fraction of the 1.2 µm filtrate (and also usually that collected with 0.8 and 0.45 µm membranes) was determined by ashing at 550°C for 24 h. Rock scrapings were also collected from the Avon, the Wylye and one of its tributaries, as well as from Wellow Brook, and their organic weight determined after drying and ashing under the conditions described above.

The weight of a number of algal species was estimated from virtually pure growths found in local rivers and ponds at different times of the year. Several other species were isolated from mixed populations by pipetting. These were placed in 100 ml Pyrex flasks containing filtered pond water and held at a constant level of illumination of approximately 1,000 lux. In all instances the size of cells was comparable to those growing in rivers. Occasionally, however, it was not possible to either grow substantial cultures of certain common algal species or to find relatively pure populations in nature.

Results

Avon River

The dry weight of suspended solids collected through membranes with a pore size of 1.2 µm fluctuated greatly during the investigation (Fig. 53). The highest values, i.e. greater than 20 mg l^{-1}, always occurred during flood conditions while low values, i.e. less than 1.0 mg l^{-1}, were associated with relatively low water levels and could be found at all times of the year. The organic content of this material also exhibited wide fluctuations, i.e. from 0.2 - 15.9 mg l^{-1}. The dry weight of suspended solids collected with 0.45 and 0.8 µm membranes normally exceeded by up to 30% the values obtained with the 1.2 µm membrane. With respect to material attached to rocks in the River Avon, the fluctuations in the dry weight bore considerable similarity to those outlined for algal numbers (Fig. 54). Maximum levels, 20 mg cm^{-2}, were recorded during the autumn of 1973 while in 1974 the highest levels, 14 mg cm^{-2}, occurred in the spring. The same trends were observed in the organic content of the above material which ranged from 0 - 10 mg cm^{-2}.

Expressing the organic dry weight of the common planktonic species (Table24) as a percentage of the organic fraction of the total suspended material collected with 1.2 µm membranes gave values which ranged from between 0.9 and 80%. The lowest levels invariably occurred during the winter but a gradual increase took place reaching a maximum during the mid-summer blooms of Stephanodiscus hantzschii. Assuming that the percentage organic material in the suspended solids collected with 0.45 and 0.8 µm membranes is similar to that outlined for 1.2 µm filters, algae represented from 0.7 to 55% of the organic material. The epilithic flora on the other hand accounted for only 1 - 4% of the organic material attached to the rocks.

River Wylye

The dry weight of suspended solids collected from the River Wylye with 1.2 µm membranes ranged from 2 to 42.5 mg l^{-1} with the lowest and highest values occurring during the winter and summer respectively (Fig.55). As with the Avon samples, the fluctuations in the organic content of this material (0.5 - 18.2 mg l^{-1}) followed much the same

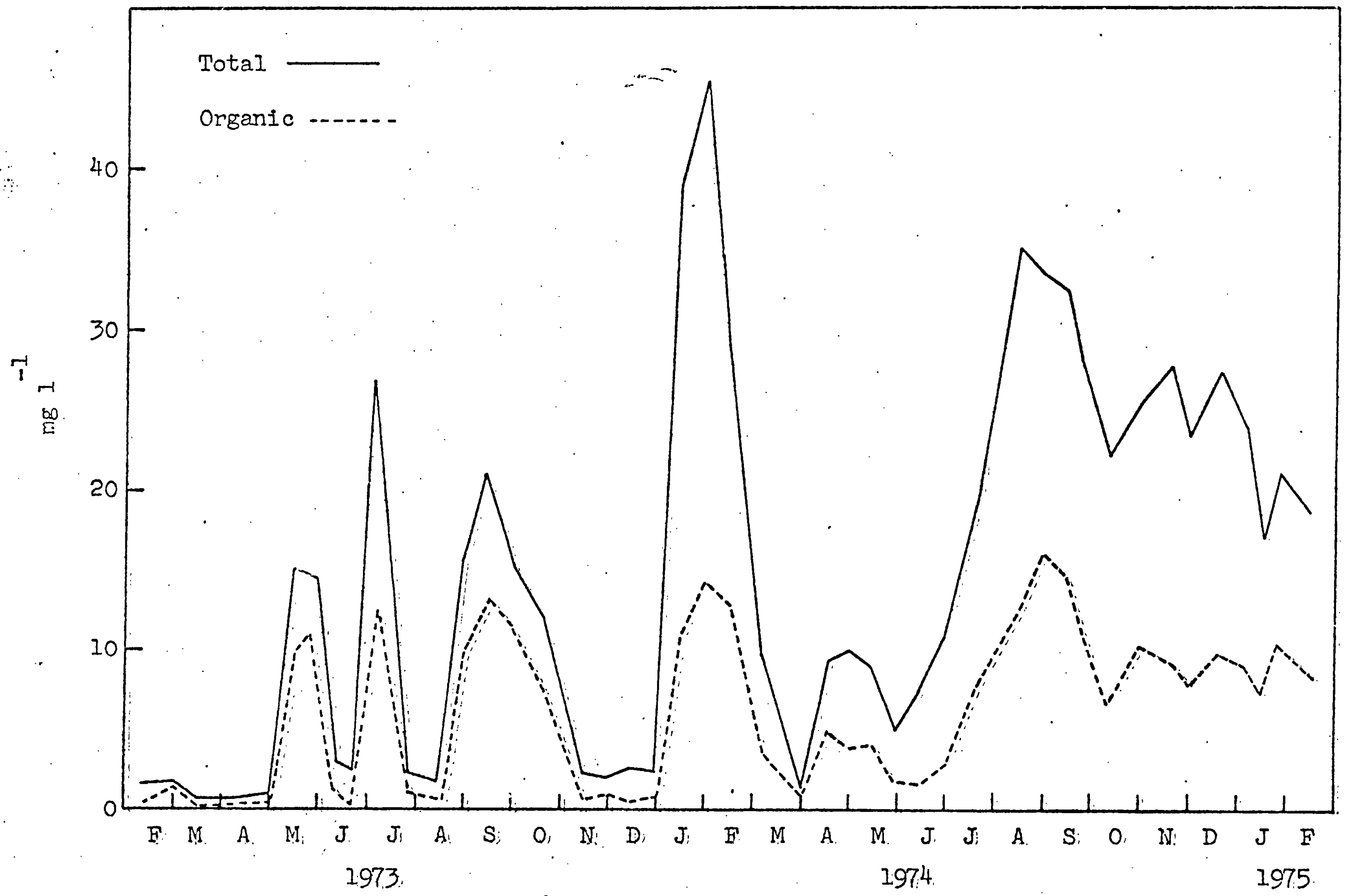

Fig. 53. Seasonal changes in the dry weight of suspended solids filtered through 1.2 µm Sartorius membranes in the Avon River.

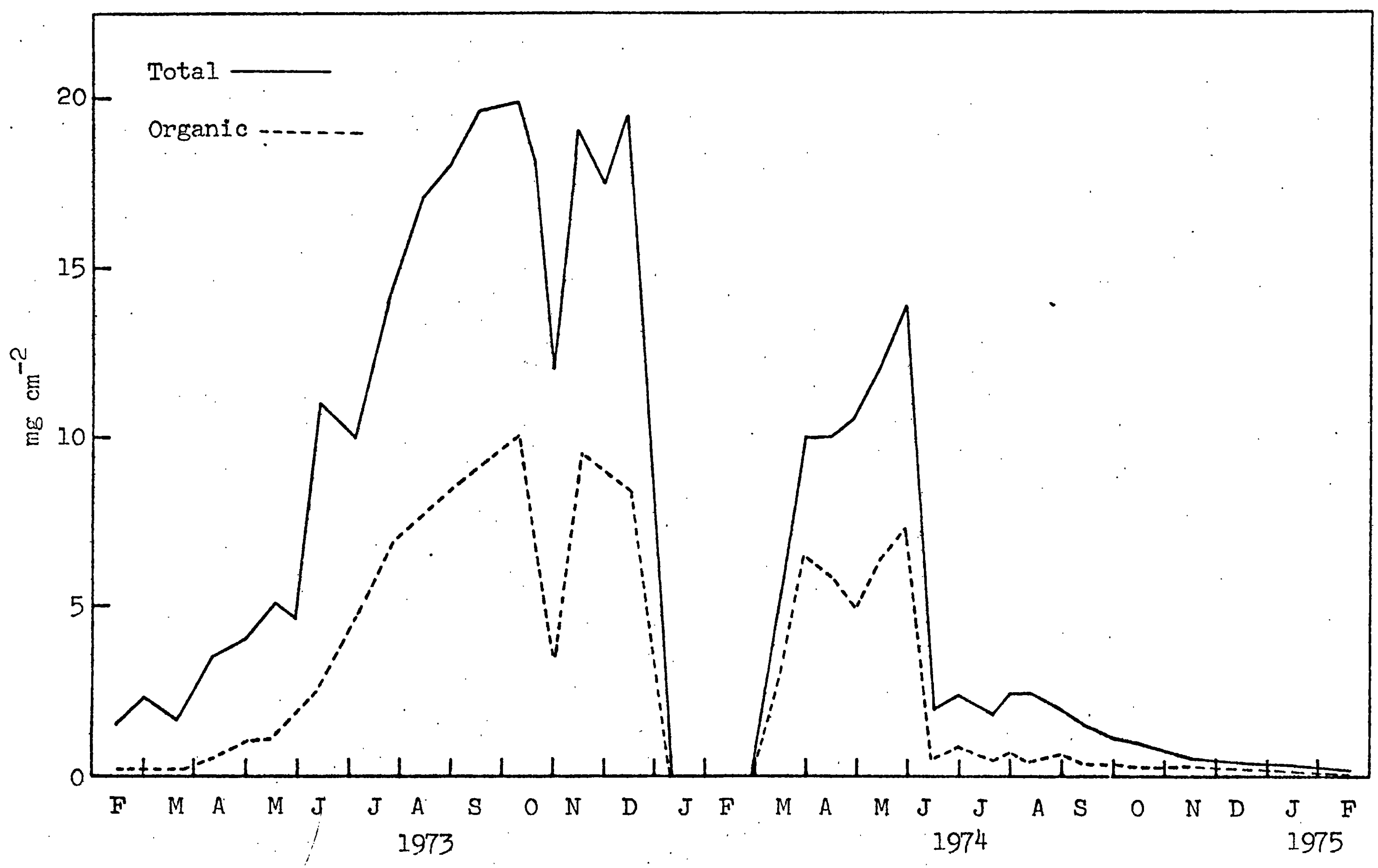

Fig. 54. Seasonal changes in the dry weight of material attached to rocks in the Avon River.

Table 24. The total dry weight and the weight of only the organic fraction of some common species of algae grown in the laboratory and collected from natural poulations.

Cultured Populations	Weight (mg x 10^6 cells^{-1})		Average Cell length (μm)
	Total	Organic	
Achnanthes lanceolata	0.23	0.13	15
Achnanthes minutissima v. cryptocephala	0.03	0.02	10
Gomphonema olivaceum	0.35	0.14	30
Gomphonema parvulum	0.29	0.14	25
Melosira varians	0.29	0.15	40
Stephanodiscus hantzschii	0.16	0.09	20
Chlamydomonas monadina	0.17	0.15	15
Natural populations			
Diatoma vulgare	0.73	0.31	45
Navicula viridula	0.69	0.39	45
Nitzschia dissipata	0.24	0.15	25
Nitzschia palea	0.22	0.13	40
Rhoicosphenia curvata	0.33	0.16	30
Surirella ovata v. minuta	0.68	0.30	30
Scenedesmus dimorphus	0.11	0.10	20
Phormidium foveolarum	0.07	0.06	50

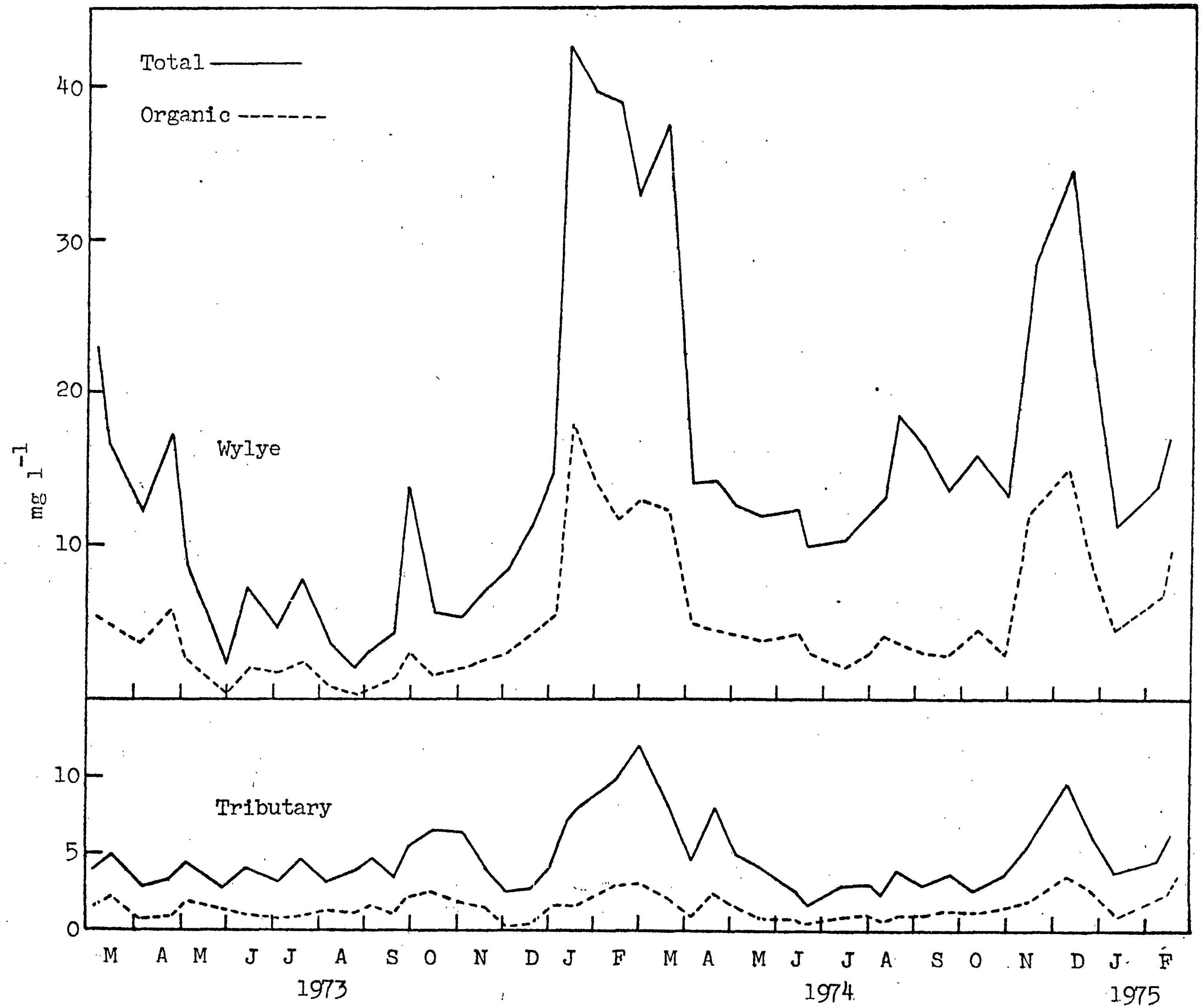

Fig. 55. Seasonal changes in the dry weight of suspended solids filtered through 1.2 µm Sartorius membranes in the River Wylye and one of its tributaries.

pattern as that exhibited by the total fraction. Although the dry weight of suspended solids collected with 0.8 and 0.45 μm membranes always exceeded that obtained by the 1.2 μm filter by up to 30 and 55% respectively, the proportion of organic material remained relatively similar. A comparatively smaller quantity of suspended solids (1.7 - 12 mg l^{-1}) was collected with 1.2 μm membranes in the tributary where the amount of organic material ranged from 0.3 - 3.7 mg l^{-1} (Fig. 55).

The dry weight of material attached to the rocks in the Wylye fell gradually from 6 mg cm^{-2} in March 1973 to 0.5 mg cm^{-2} in March 1974 but then increased sharply to 12 mg cm^{-2} in July only to fall again to low levels in the autumn and winter (Fig. 56). A similar pattern of change was observed for the organic fraction with values ranging up to 6.1 mg cm^{-2}. However, much higher levels, fluctuating betwen 90 and 1350 mg cm^{-2} of the total dry weight and 30 and 850 mg cm^{-2} for the organic fraction, were recorded from the tributary of the Wylye and these showed great variation between different months.

During the summer of 1973, when the weight of suspended solids in both the Wylye and its tributary remained relatively low but the standing crop of the plankton was exceptionally high, algae accounted for 7 - 10% of the organic material filtered through the 1.2 μm membranes. However, during the flood of January and February 1974, when the amount of solids was very high and the standing crop low, this level never exceeded 0.5%. Since the weight of one of the most common epilithic species, Amphora ovalis v. pediculus, was not available, data are presented only for the months when Phormidium foveolarum predominated i.e. between June and August 1974. During this latter period, algae represented from 0.5 - 2% of the attached organic material. In the tributary, the highest value, 1.4% , occurred during the spring bloom of 1973 while during the same period in 1974 algae represented only 0.01% of the total organic matter.

Kennett and Avon Canal

The dry weight of suspended solids collected with 1.2 μm membranes from the Kennett and Avon Canal ranged from 3.5 - 15.9 mg l^{-1} during the summer months and from 5.8 - 17.0 mg l^{-1} during the winter (Fig. 57). The organic content of this material exhibited similar patterns of change with minimum and maximum values of 1.0 and 8.9 mg l^{-1}

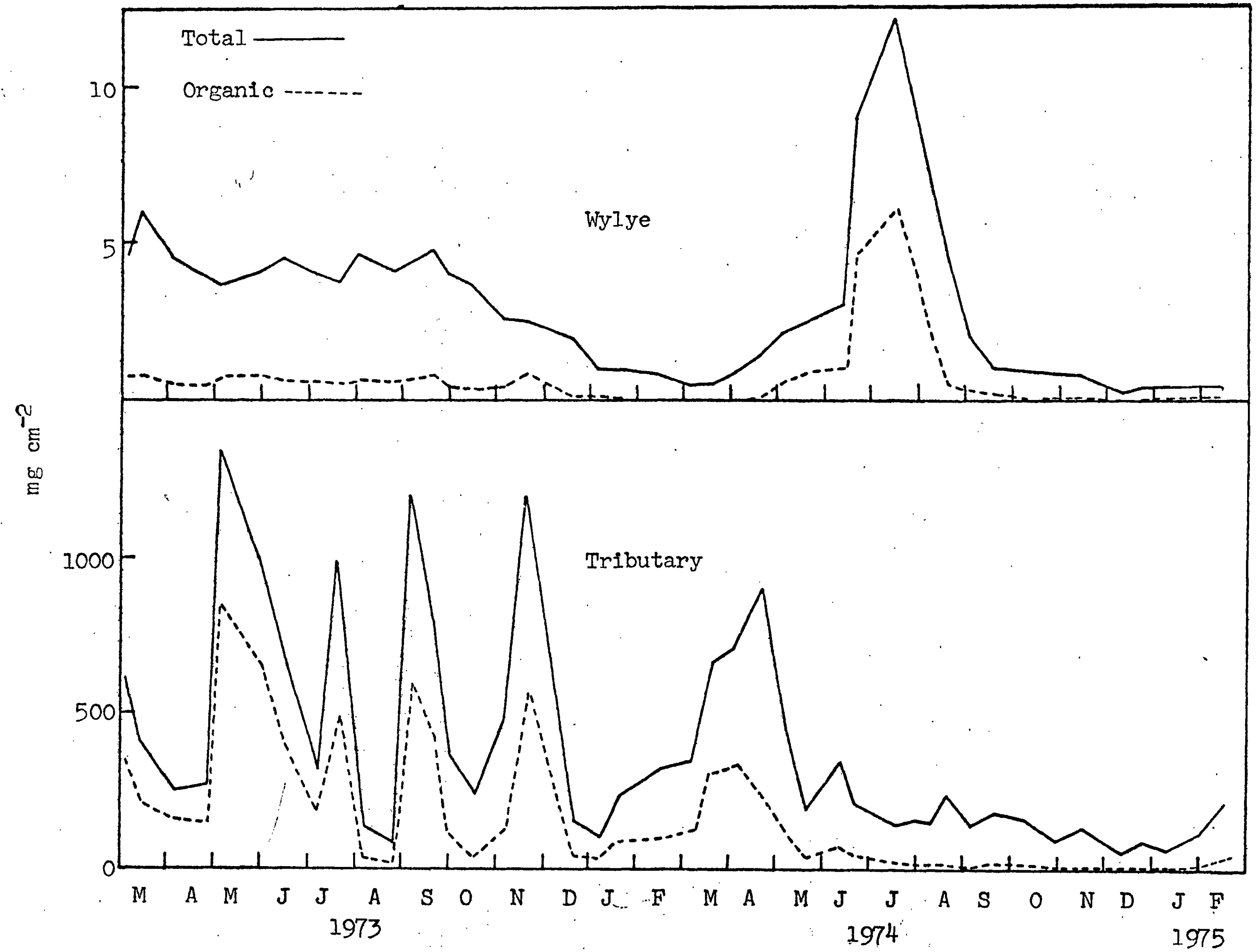

Fig. 56. Seasonal changes in the dry weight of material attached to rocks in the River Wylye and one of its tributaries.

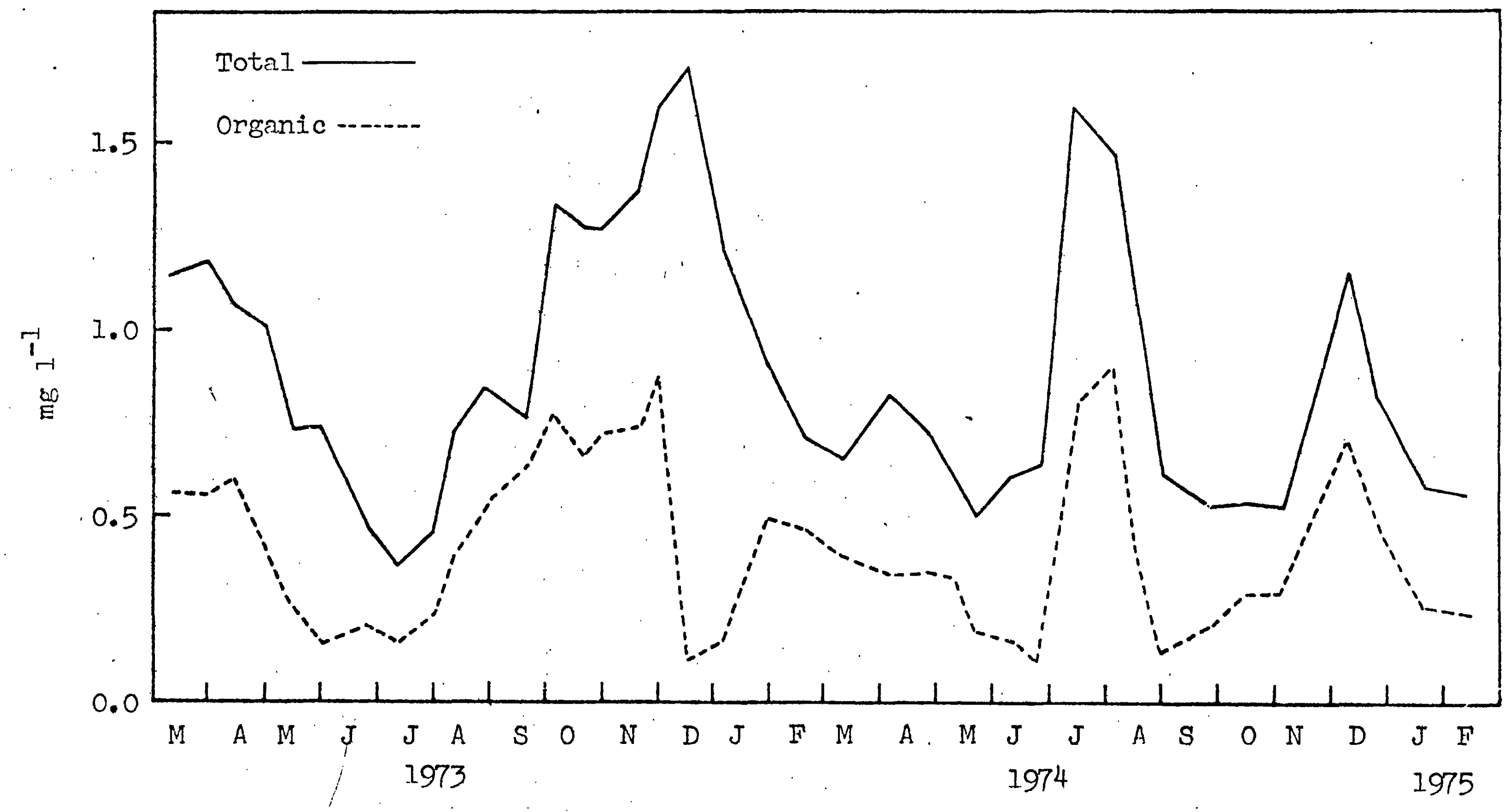

Fig. 57. Seasonal changes in the dry weight of suspended solids filtered through 1.2 µm Sartorius membranes in the Kennett and Avon Canal.

respectively. The weight of suspended solids collected with 0.8 and 0.45 µm membranes was almost invariably clearly greater than that described above but the seasonal trend remained unchanged. The organic fraction, expressed as a percentage of the total dry weight, was similar to that described for the 1.2 µm membranes.

Since the weight of one of the most common planktonic taxa in the canal, *Trachelomonas volvocina* v. *minuta*, could not be obtained, data are only presented for the months in which this form was scarce. The greatest contribution algae made to the organic weight of the suspended solids collected with 1.2 µm membranes was 0.3%, this occurring during March 1974 when *Chlamydomonas monadina* predominated. At other times of the year, values were much lower, sometimes averaging as little as 0.05%. Expressing the amount of algae as a proportion of the collections made with 0.8 and 0.45 µm membranes gives maximum values of about 0.20 and 0.25% respectively.

Wellow Brook

In Wellow Brook, the amount of material attached to rocks fluctuated greatly with maximum and minimum values of 19 and 1 mg cm^{-1} occurring during March and December 1974, respectively (Fig.58). Changes in the weight of the organic fraction followed much the same pattern with extreme values of 7 and 0.3 mg cm^{-2}.

The weight of a relatively large but rare diatom, *Navicula tripunctata*, is unknown. However, assuming that the weight is similar to that of a closely related species, *Navicula viridula*, which is of comparable volume, algae were estimated as representing less than 3% of the organic material attached to the rocks, with a maximum value of 10% occurring near the first week of April 1974.

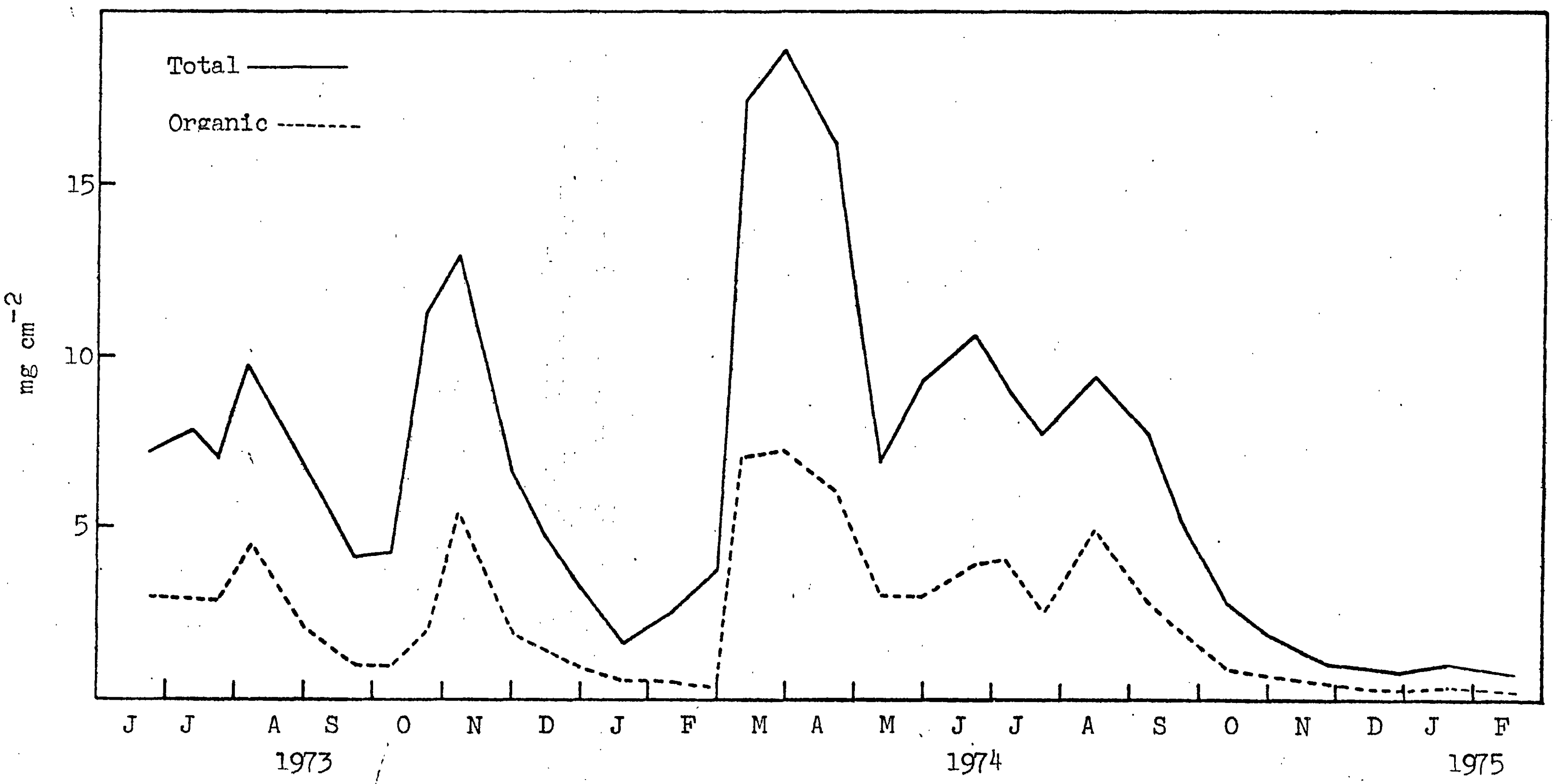

Fig. 58. Seasonal changes in the dry weight of material attached to rocks in Wellow Brook.

Discussion

Since, as indicated in Section 4 , the proximate composition of algae may vary between samples taken at different times of the year, the application of a standard weight to a particular species of known volume may involve a variable degree of inaccuracy. It is important to note, however, that as these fluctuations would not, from the data presented in Section 4 , be greater than 17%, they could not distort the overall picture presented in the present investigation.

The major point arising from this study is that algae normally make a small contribution to the organic weight of both suspended and attached material found in eutrophic rivers of southern England. Although phytoplankton and phytobenthos likewise play only a small role in the energy cycle of oligotrophic streams and lakes (Darnell, 1964; Minshall, 1967; Efford, 1969), their relatively small contribution to the solids in the rivers in this study is perhaps surprising in view of the relatively high density of algae at the sites investigated. This finding implies that an increase in algal populations tends to be associated with an elevation in the amount of allochthonous material. Since, in this study, algae were a relatively more important component of the suspended solids in the Avon, the much larger amount of water has apparently diluted the allochthonous material flowing into this system. This situation parallels to some extent that found in large lakes and oceans where the microflora are a major food source for herbivores (Prescott, 1962). As might be expected, algae were of greatest importance during periods of maximum standing crop, i.e. usually during the spring bloom, while under flood conditions they invariably formed an insignificant part of the total organic material in the rivers.

4. Seasonal Changes in the Proximate and Fatty Acid Composition of some Naturally Grown Freshwater Algae

Introduction

Although a large number of aquatic animals feed on algae, the literature dealing with the nutritional value of this food is limited essentially to cultures grown in the laboratory (Harris and Riley, 1956; Parsons, 1963; Chau, Chuecas and Riley, 1967; Ackman, Tocher and McLachlan, 1968; Demort et al., 1972; Platt and Irwin, 1973). The purpose of this study was therefore to describe seasonal changes in the protein, lipid, ash, cellulose and carbohydrate content (i.e. proximate analyses) and the fatty acid composition of some naturally grown algae.

Materials and Methods

Entire filaments of Cladophora glomerata, Ulothrix zonata and Spirogyra sp. were collected every two weeks from virtually pure growths found in unshaded reaches of Wellow Brook, the Kennett and Avon Canal and the Avon River respectively. Samples of Scenedesmus dimorphus and Cosmarium laeve were taken every two weeks from virtually pure populations (greater than 90% by volume) growing in unshaded rain-fed tanks located on the University of Bath campus. The filamentous taxa were washed with distilled water to remove adherent material while the Scenedesmus and Cosmarium populations were filtered through Millipore membranes (pore size 1.2 µm) and resuspended in a small volume of distilled water to allow sand and detritus to settle. Microscopic examination indicated that all five samples were almost pure although small quantities of detritus occurred among the Scenedesmus and Cosmarium collections.

Each collection of algae was dried by sublimation in a Leybold-Heraeus GT 2 Freeze Drier. Total lipids in one 1 - 1.5 g subsample of each species were extracted by leaving the material overnight in 100 ml chloroform : methanol (2:1 , vol: vol) followed by homogenation of the entire sample for three minutes. Thereafter, the organic solvents were evaporated using a Buchler Rotary-Evapomix and the lipid extract dried to constant weight by sublimation. The phospholipid fraction of each species was determined by ashing duplicate lipid aliquots of 1.5 mg with sulphuric and perchloric acids (3:2 , vol : vol), estimating the total weight of phosphorous and multiplying the value by 25 (Chen, Toribara and Warner, 1956). The fatty acids of both the phospho- and neutral lipids were determined as described by Hunter and Rose (1972), except that the nitrogen carrier flow rate was increased to 90 ml min^{-1}. The total protein (Fels and Veatch, 1959) and cellulose (Updergraff, 1969) content of each species was also determined while 1 - 1.5 g subsamples were used for ashing, which was conducted at 550^0C for 24 h. The nitrate-nitrogen and orthophosphate-phosphorus content of the river and tank water were determined as previously outlined (see page 6). Water temperature and pH were taken during the early afternoon on each collection day.

Results

Physico-chemical analyses:

Relatively high levels of NO_3-N and P_2O_5-P (Tables 1,17,20) were maintained throughout the study at all locations. No consistent pattern of seasonal variation appeared among the different sites and little correlation existed with standing crop. The pH, ranging from 7.5 - 8.5 , fluctuated inconsistently at all localities although the lowest values occurred in winter. Temperatures are presented in Figs 59 - 63.

Proximate analyses:

The protein content of Cladophora glomerata fluctuated without any apparent pattern about a mean level of 12.4% (range 9.8 - 15.0%) of the dry weight of the algae (Fig.59). The total lipid, which averaged 15.0%, rose from 7.0% in September to a peak of 25.2% during October and November, coincident with a fall in standing crop and temperature. This period represented the time when major fluctuations were occurring, the extreme values encompassing those found at any other time of the year. Ash, averaging 22.0% (range 13.3 - 32.5%), peaked during both the summer and winter , while cellulose reached their highest levels (23 - 24%) during the winter. The average amount of cellulose throughout the year was 17.8% and the smallest values, 13.0%, occurred early in September. The chemical nature of the remaining fraction of the Cladophora sample, ranging from 20 - 51% of the dry weight (average 32.8%), was not determined by analytical procedure. It is probably safe to assume, however, that at least most of this component was carbohydrate.

Ulothrix zonata contained considerably less protein than Cladophora with an average of only 8.0% (Fig.60). The lowest levels (3.5%) occurred during mid winter, concurrent with a small standing crop, while the maximum value of 12.5% was recorded early in June. Total lipids were also relatively low (average 11.9%; range 4.2 - 19.3%) , reaching maxima in the spring, coincident with a high standing crop, while most of the low values were observed in the winter. The ash values were slightly higher than in Cladophora with a mean of 24.0%. The highest levels (35 - 36%) invariably occurred in the spring while

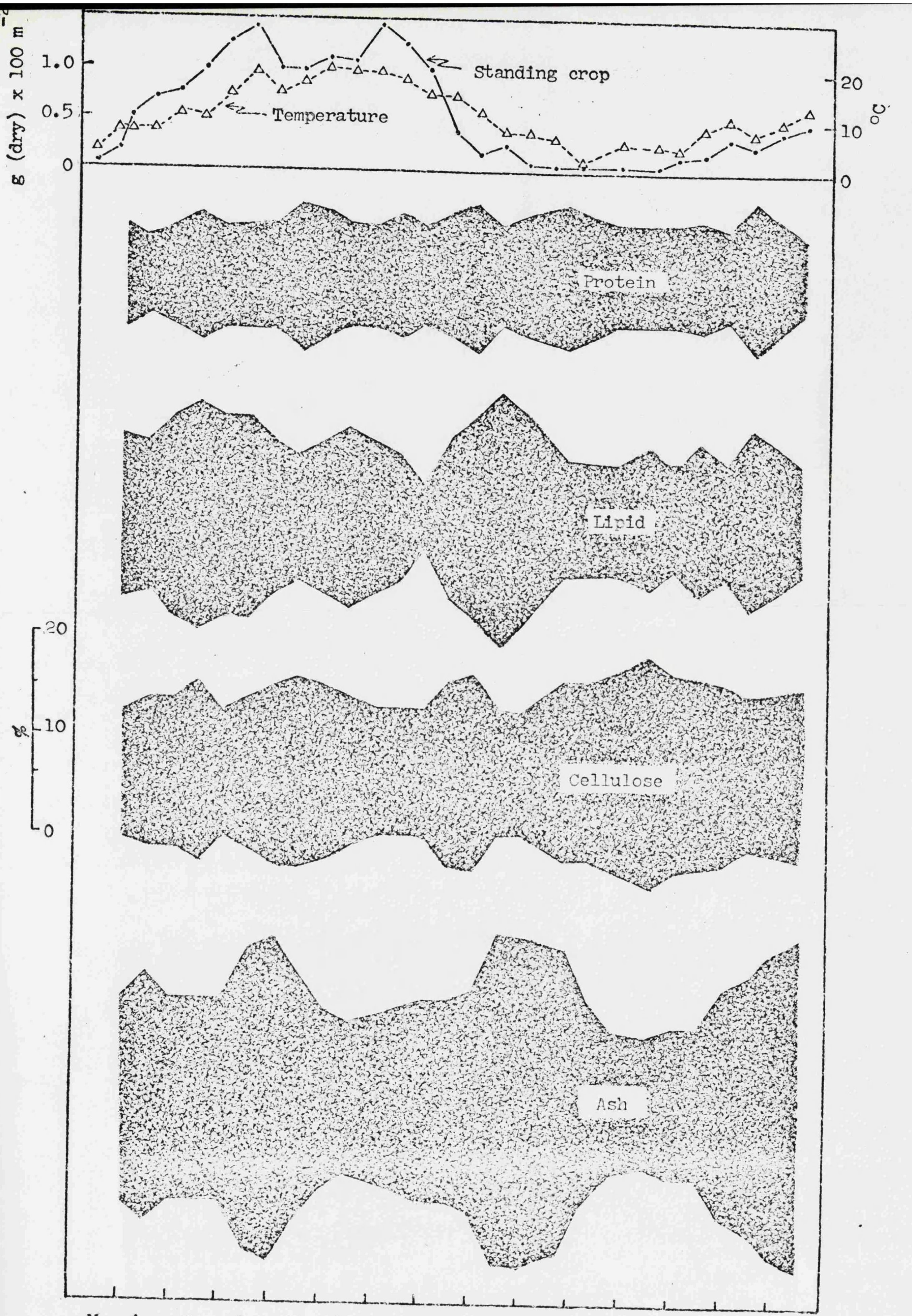

Fig. 59. Seasonal changes in the amount of protein, lipid, cellulose and ash, expressed as a percentage of the total dry weight, in Cladophora glomerata together with changes in the standing crop and water temperature.

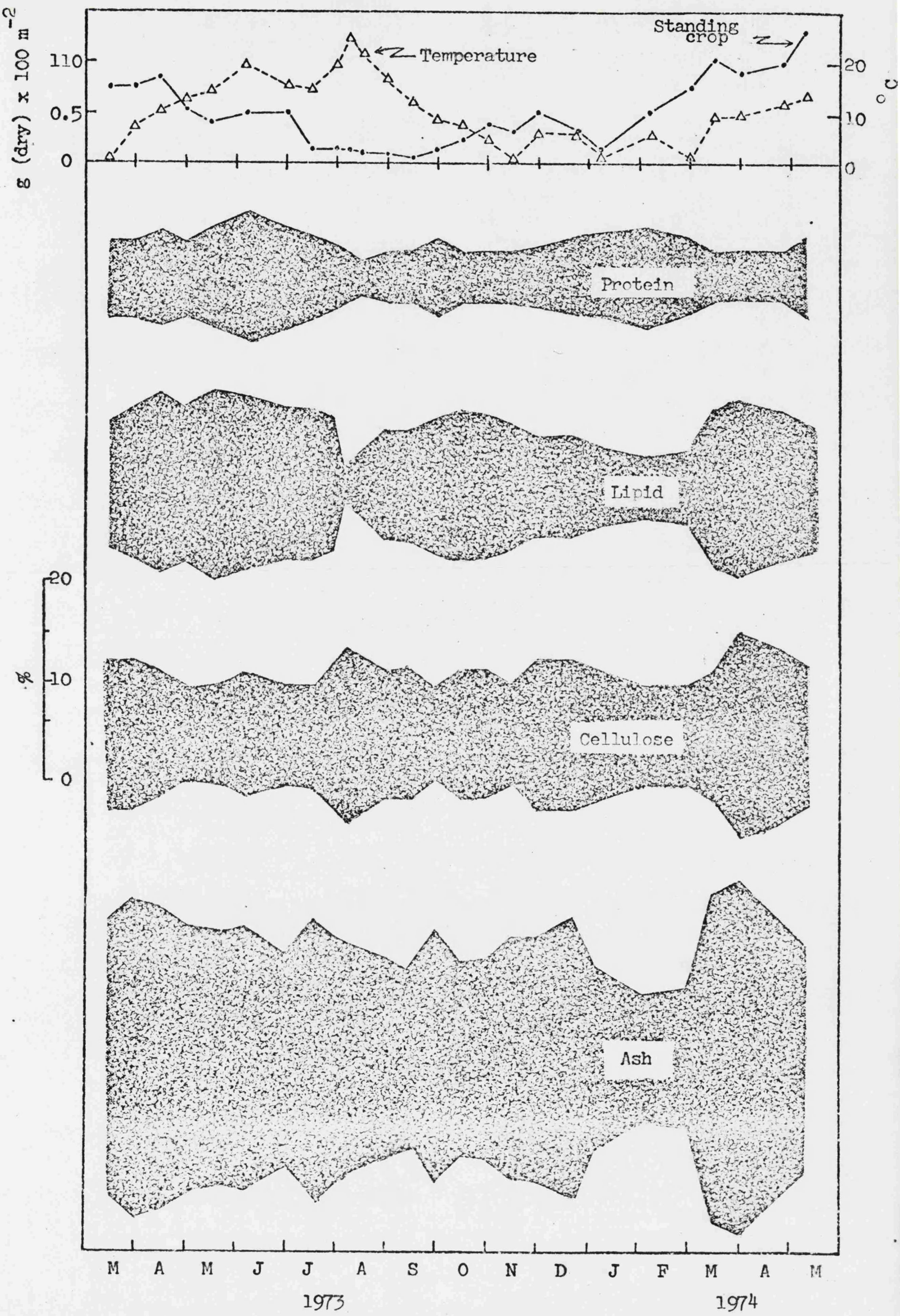

Fig. 60. Seasonal changes in the amount of protein, lipid, cellulose and ash expressed as a percentage of the total dry weight, in Ulothrix zonata together with changes in the standing crop and water temperature.

the lowest (12 - 13%) were found during the winter. The remaining fraction of Ulothrix was not analyzed but once again it is probably safe to assume that most of this substance was carbohydrate. The average value for the year (43%) was relatively high with maximum and minimum levels of 62 and 22% respectively.

The protein (average 12.4%; range 6.1 - 20.2%), lipid (average 16.1%; range 10.8 - 20.5%) and cellulose (average 10.0%; range 4.6 - 16.5%) fractions of Spirogyra sp. showed little consistent pattern of seasonal change (Fig.61). On the other hand, ash (average 14.6%; range 10.0 - 27.5%) rose to a well defined peak during the winter, coincident with a low standing crop. Carbohydrates averaged 56% , with maximum and minimum levels of 64 and 33% respectively.

The protein level of Scenedesmus dimorphus was slightly greater than that of the filamentous taxa averaging about 13% (Fig.62). Well defined peaks up to 17.5% were observed during the spring and late summer while the lowest levels, 8.0% , occurred during mid winter. Total lipids were high, averaging 29.5% (range 16.4 - 40.3%). There was no apparent pattern to the seasonal variations with maximum levels occurring during the spring and late summer and the minimum levels being exhibited in mid summer and the autumn. Both the ash (average 9.8%; range 6.2 - 14.8%) and cellulose (average 9.8%; range 6.5 - 20.0%) levels, which were considerably lower than those of the filamentous taxa, showed no apparent seasonal pattern. Carbohydrates averaged 41.5% with maximum and minimum values of 51.5 and 21% respectively.

The relative amounts of the different constituents of Cosmarium laeve were approximately the same as those of Scenedesmus (Fig. 63). Protein (average 15.0%; range 11.5 - 20.1%) and total lipid (average 22.5%; range 15.0 - 33.3%) occurred in relatively large quantities while ash (average 8.2%; range 4.8 - 12.5%) and cellulose (average 7.5%; range 4.5 - 13.0%) were relatively low. Carbohydrate ranged from approximately 32 to 60% with an average value of 46.8%.

Phospholipid and fatty acid analyses:

Cladophora contained the greatest amount of phospholipid, averaging 10.0% (range 8.2 - 13.3%) by weight of the total lipid, followed by Cosmarium (average 7.9%; range 5.8 - 10.0%), Ulothrix (average 7.1%; range 5.1 - 9.8%) , Spirogyra (average 6.3%; range 5.5 - 8.9%) and Scenedesmus (average 5.2%; range 4.3 - 7.2%). A distinct pattern of seasonal variation in the amount of phospholipid

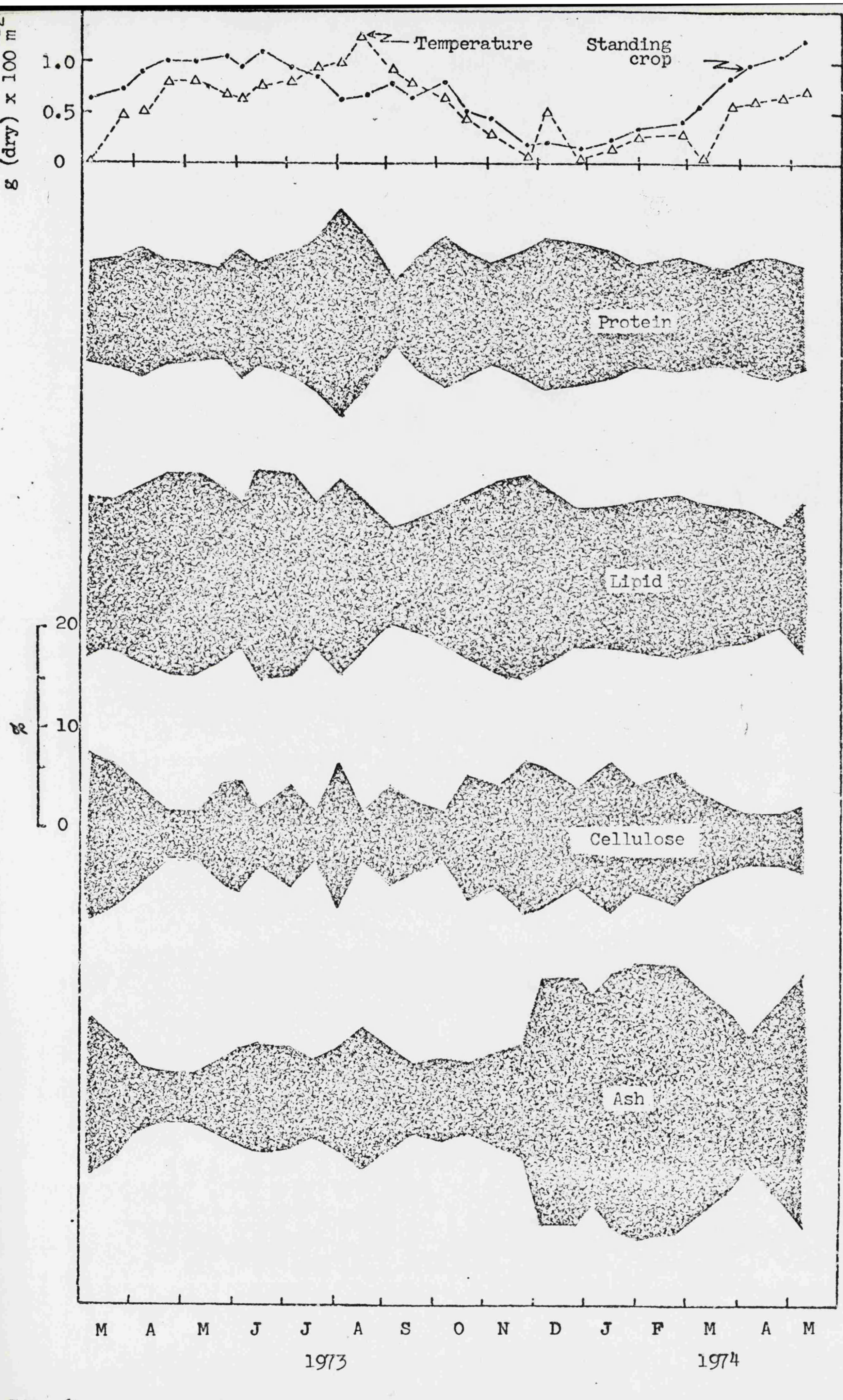

Fig. 61. Seasonal changes in the amount of protein, lipid, cellulose and ash, expressed as a percentage of total dry weight, in *Spirogyra* sp. together with changes in the standing crop and water temperature.

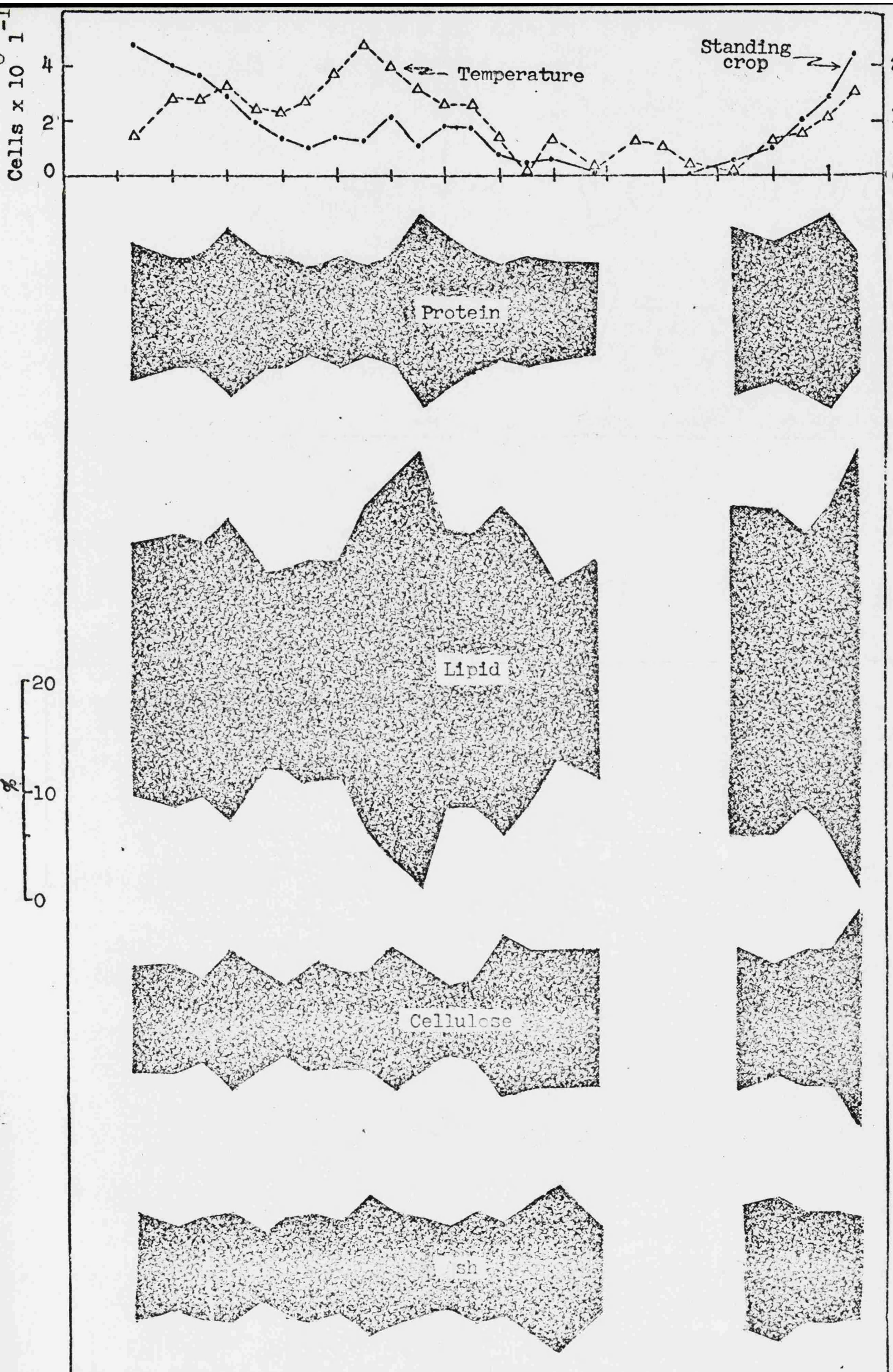

Fig. 62. Seasonal changes in the amount of protein, lipid, cellulose and ash, expressed as a percentage of the total dry weight, in Scenedesmus dimorphus together with changes in the standing crop and water temperature. Insufficient

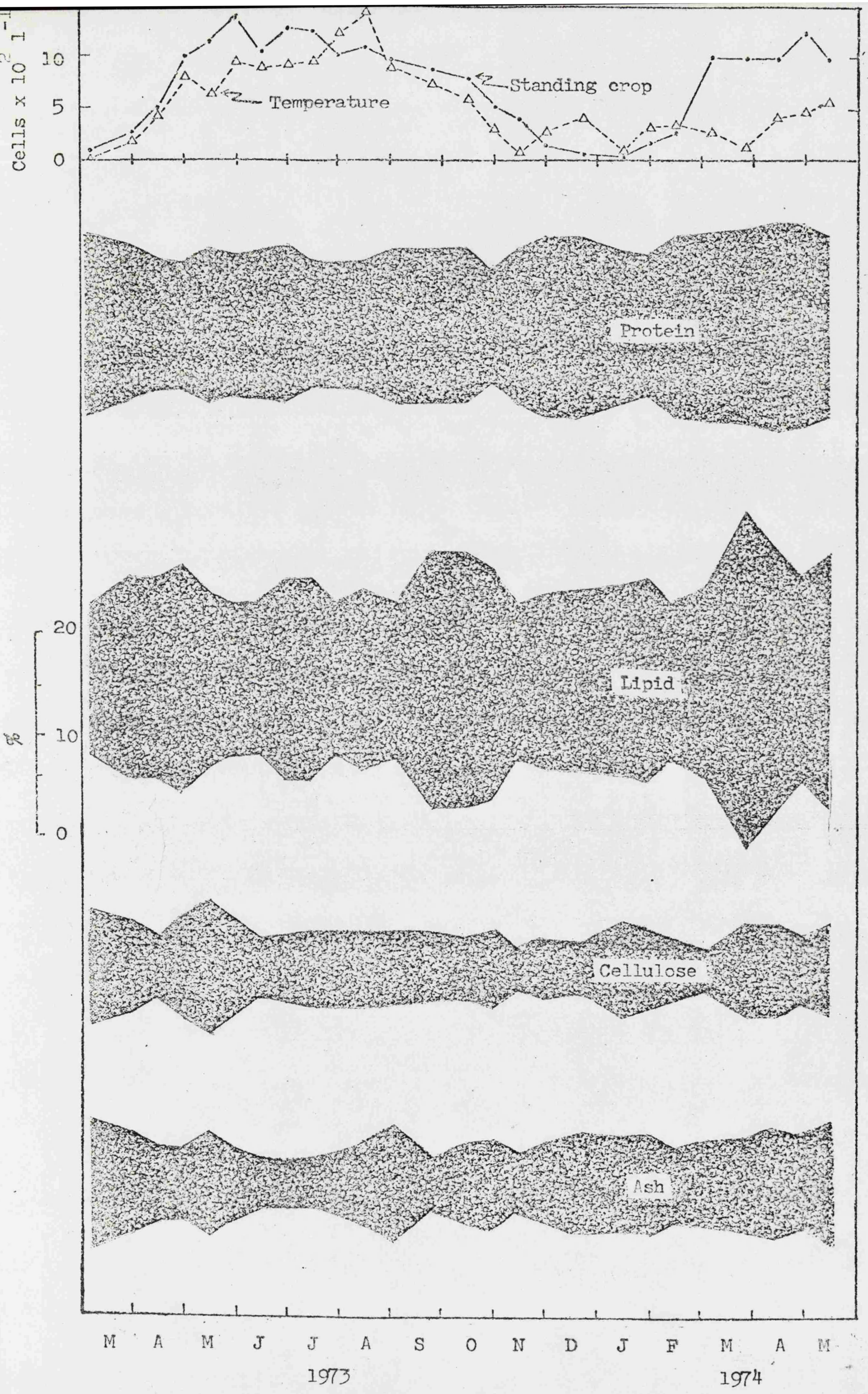

Fig. 63. Seasonal changes in the amount of protein, lipid, cellulose and ash, expressed as a percentage of the total dry weight, in Cosmarium laeve together with changes in the standing crop and water temperature.

was not evident for any species. In all species, the predominant fatty acid of the phospholipids was 18:1 (Table 25). The second most common among the filamentous taxa was usually 18:2 followed by 18:3 and 16:1. In Scenedesmus and Cosmarium, however, the last of these was second in abundance but with 18:2 and 16:0 also being important. The concentration of the different fatty acids varied considerably with the time of year. Thus, palmitic acid (16:0), the most notable example of this seasonal variation, accounted in August for less than 3% of the total fatty acids regardless of species while, at other times of the year, it usually represented at least 15%. Similarly, 18:1 showed a drop during the colder months, particularly in the case of Scenedesmus and Cosmarium.

The predominant neutral lipid fatty acids were 18:1 and 16:1 , followed by 16:0 and 14:0 (Table 26). As with the phospholipids, 16:0 was unusually rare in August rising to much higher levels at other times of the year. In addition, the concentration of 16:1 usually showed a sharp rise during the colder months while the relative amount of 18:1 in all five species fell.

Table 25. The percentage molar concentration of fatty acids in the phospholipids of *Cladophora glomerata*, *Ulothrix zonata*, *Spirogyra* sp., *Scenedesmus dimorphus* and *Cosmarium laeve* at different times of the year.

Fatty Acid	Cladophora				Ulothrix				Spirogyra			
	Aug.	Nov.	Jan.	Apr.	Aug.	Nov.	Jan.	Apr.	Aug.	Nov.	Jan.	Apr.
14:0	10.9	7.8	9.1	6.3	9.4	6.3	9.1	4.5	13.1	9.8	11.1	10.0
15:0	0.7	0.8	1.3	1.1	1.0	0.5	1.2	0.7	0.4	2.2	1.1	0.5
16:0	1.9	16.3	16.2	19.6	1.5	2.5	16.3	24.1	2.9	4.3	9.8	14.4
16:1	4.8	5.3	8.9	5.7	14.6	18.1	10.3	16.1	7.8	16.1	8.5	15.9
16:2	0.0	0.1	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.2	0.1	0.0
18:0	4.0	2.2	3.2	2.8	5.9	4.5	3.2	0.1	9.3	3.2	4.5	1.1
18:1	31.2	26.2	27.6	19.4	38.8	35.9	30.2	22.0	34.0	27.8	30.3	20.0
18:2	16.8	14.3	17.1	9.9	16.3	14.9	16.2	11.9	22.5	19.9	22.5	13.1
18:3	19.7	20.1	13.2	31.2	2.4	13.3	9.8	12.6	2.3	13.1	9.2	16.0
20:3	0.0	0.3	0.0	0.0	4.1	0.0	0.0	0.5	0.0	0.0	0.5	0.5
20:5	8.5	4.5	3.1	2.2	2.3	1.5	3.1	5.0	6.2	1.1	0.5	1.2
22.6	1.5	2.1	0.2	1.7	0.7	2.5	0.5	2.5	1.5	2.3	1.9	1.5

Table 25 (cont'd)

Fatty Acid	*Scenedesmus*				*Cosmarium*			
	Aug.	Nov.	Jan.	Apr.	Aug.	Nov.	Jan.	Apr.
14:0	11.3	10.9	9.3	8.3	6.1	9.0	7.7	6.2
15:0	1.2	0.8	0.9	1.1	0.7	0.8	1.2	1.5
16:0	1.1	16.3	18.2	22.3	1.4	13.8	19.2	25.2
16:1	14.3	19.2	20.1	18.2	18.7	20.0	21.0	22.6
16:2	0.0	1.1	0.1	0.1	0.0	0.5	0.5	1.0
18:0	3.9	4.2	3.1	0.1	6.2	4.9	5.8	0.5
18:1	35.2	12.2	14.4	20.2	38.4	27.2	14.0	15.2
18:2	17.8	18.3	17.8	9.7	16.3	15.8	17.2	10.5
18:3	6.5	12.2	9.8	13.0	4.9	3.0	9.3	13.0
20:3	1.0	0.5	0.7	0.5	0.0	0.3	0.1	0.1
20:5	6.5	3.1	4.1	3.2	6.2	3.2	1.9	1.5
22:6	1.2	1.2	1.5	3.3	1.1	1.5	2.1	2.7

Table 26. The percentage molar concentration of fatty acids in the neutral lipids of _Cladophora glomerata_, _Ulothrix zonata_, _Spirogyra_ sp., _Scenedesmus dimorphus_ and _Cosmarium laeve_ at different times of the year.

Fatty Acid	Cladophora				Ulothrix				Spirogyra			
	Aug.	Nov.	Jan.	Apr.	Aug.	Nov.	Jan.	Apr.	Aug.	Nov.	Jan.	Apr.
14:0	16.5	13.8	16.2	14.2	12.3	9.8	11.3	8.3	14.4	13.9	14.0	13.1
15:0	0.7	3.9	0.9	5.3	1.9	2.2	3.3	3.9	0.6	3.2	1.8	4.4
16:0	2.9	19.3	13.7	23.8	1.3	23.1	19.8	25.5	6.1	19.3	22.1	20.2
16:1	19.9	20.3	25.2	26.6	7.9	13.3	19.8	20.0	17.5	19.9	26.2	25.3
16:2	0.0	0.5	0.6	1.5	0.0	0.3	0.5	1.0	0.0	0.0	0.0	0.5
18:0	12.8	13.3	9.2	1.1	9.9	3.9	8.7	2.5	6.5	1.2	0.5	1.0
18:1	26.7	12.8	13.9	15.5	42.0	27.0	15.7	19.4	42.5	29.5	27.2	17.3
18:2	16.2	9.2	10.3	0.0	7.9	9.8	5.2	4.6	6.5	4.2	3.1	5.2
18:3	1.5	6.2	7.3	8.1	4.4	6.2	7.9	8.8	3.1	4.5	3.2	6.0
20:3	0.0	0.5	0.3	0.0	1.0	0.1	0.0	0.8	0.5	1.0	0.0	0.0
20:5	1.6	0.1	2.2	2.0	8.6	2.8	7.3	2.0	2.3	0.5	1.1	4.1
22:6	1.2	0.1	0.2	1.9	2.8	1.2	0.5	3.2	0.0	2.8	0.8	2.9

Table 26 (cont'd)

Fatty Acid	Scenedesmus				Cosmarium			
	Aug.	Nov.	Jan.	Apr.	Aug.	Nov.	Jan.	Apr.
14:0	9.6	9.2	8.9	8.8	3.0	3.3	2.5	3.1
15:0	1.1	2.3	3.0	3.2	1.1	1.0	1.5	2.2
16:0	2.5	19.3	22.1	20.9	2.4	19.3	12.1	20.9
16:1	14.3	17.8	20.9	26.1	19.8	18.7	20.2	26.3
16:2	0.0	0.1	0.1	0.1	0.0	0.3	0.4	0.5
18:0	11.3	8.2	9.3	0.5	17.1	18.3	15.6	1.0
18:1	40.5	29.3	15.2	19.1	32.3	14.2	15.2	16.3
18:2	7.8	7.3	8.2	6.3	6.3	6.4	7.0	6.5
18:3	5.4	3.2	7.3	11.0	6.3	8.3	18.7	19.9
20:3	1.2	1.1	0.0	0.0	6.0	5.5	1.7	0.0
20:5	5.0	1.2	3.5	1.0	3.5	3.2	3.1	2.3
22:6	1.3	1.0	1.5	3.0	2.2	1.5	2.0	1.0

Discussion

This study clearly demonstrates that the proximate composition of the filamentous taxa differs markedly from that of Scenedesmus and Cosmarium. Thus the former group of algae contained relatively larger amounts of cellulose and ash, a feature presumably correlated with their thicker cell walls. On the other hand, in the thin-walled Scenedesmus and Cosmarium, there was a relatively large amount of lipid, a substance which might give added buoyancy to these planktonic taxa. Since Cladophora has to have comparatively strong cell walls to allow it to withstand the problems of being attached in flowing water, it is not surprising that this species contained the greatest amount of cellulose of any of the plants investigated. Scenedesmus maintained slightly more ash and cellulose than Cosmarium, a feature which again reflects differences in cell wall thickness.

The fact that the ash content of Scenedesmus dimorphus was slightly higher than the 8.1% reported for laboratory cultures of the same species (Nalewajko, 1966) may either be the result of different growth conditions or due to contamination by small amounts of detritus. Other Scenedesmus spp. may contain much more ash (e.g. 18%) depending on environmental conditions (Ketchum and Redfield, 1949). Ash in the filamentous taxa was often relatively high compared to similar forms grown in culture, i.e. 20% (Nalewajko, 1966) but occurred at levels roughly comparable to those of naturally occurring macrophytes (Tan, 1970) and was much lower than that of most diatoms (Lund, 1961, 1964).

Data on the cellulose content of algae comparable to the species investigated in this study appear to be lacking. However, aquatic macrophytes consist of between 8.6 and 26.7% cellulose (Tan, 1970) while diatoms and blue-green algae possess only a small amount of this substance (Fogg, 1953).

Parsons, Stephens and Strickland (1961) reported lipid values of about 5% in planktonic green forms, considerably less than those of the species in this study, while other investigators have recorded values of up to 86% (Spoehr and Milner, 1949). As demonstrated by Spoehr and Milner (1949), the amount of lipid in any one species varies greatly with growth conditions. With respect to protein, this component was similar in all taxa, a feature possibly reflecting the ample supply of nitrogen and phosphrous (Ketchum and Redfield, 1949).

Seasonal changes in the composition of the algae normally showed no correlation with changes in temperature, standing crop, NO_3-N , P_2O_5-P or pH. However, in Spirogyra , the ash content did increase sharply during the winter, possibly indicating a depletion of major energy reserves such as lipids. Cladophora, on the other hand, showed high levels of ash during both the spring and summer as well as in the winter, possibly indicating that the rate of photosynthesis during all three periods was low. The fact that the total levels of lipid in Cladophora increased sharply as the temperature and standing crop fell, presumably represents an adaptation for building up an energy source prior to adverse conditions. Although, in laboratory experiments, high light intensity is often correlated with increased lipid deposits (Shaw, 1966), no algae in the natural populations of the present study showed sustained peaks during the summer. The levels of protein and carbohydrate were similarly unpredictable for all species. Apparently, in most instances, the large number of factors which can influence the proximate composition of algae interacted to give a generally inconsistent pattern of seasonal change.

Several aquatic animals, which feed heavily on algae, show a marked rise in lipids during the spring (Marshall, Nicholls and Orr, 1934; Lowe, Beamish and Potter, 1973). However, since the proximate composition of the algae in this study showed no similar trend, it appears that the pattern in the above animals is related to an increased availability of food through a rise in the density of algae. Since this occurs at a time when temperatures are rising, it is also coincident with an increase in the metabolic rate of the animals. As most aquatic herbivores feed heavily on unicellular or colonial algae rather than on filamentous species (Hynes, 1970; Moore and Beamish, 1973) they tend to utilize the more nutritious of the two food sources.

No correlation existed between the level of phospholipids and environmental parameters, contrasting with laboratory cultures in which these components have been found to be affected by temperature and light (Shaw, 1966). The predominant fatty acid in the phospholipids, 18:1 , was similar to that reported for the total fatty acids of other green algae (Ackman et al., 1970). Other predominant fatty acids of the filamentous forms were highly unsaturated compared to those of Scenedesmus and Cosmarium, possibly reflecting differences in metabolism and/or growth conditions. The considerable variation existing in the fatty acid concentration of the same species at different times of the year, presumably due to changing environmental conditions, illustrates the care that must be exhibited in taxonomic interpretations of metabolite analyses. The rise in the proportion of 16:0 and the reduction in 18:1 with falling levels of temperature and light is surprising since it is opposite to the pattern often exhibited in laboratory cultures (e.g. Holton, Blecker and Onore, 1964). This inverse relationship between the two fatty acids may however reflect the influence of several other environmental factors such as nutrient type and concentration on algal cultures (Nichol, 1965).

The fatty acids in the neutral lipids of the five species were similar to each other and to those reported for other algal classes (Ackman et al., 1968). Hexadecenoic acid (16:1), often predominant in the species under investigation, is normally rare in cultured green algae although it does occur frequently in large quantities in blue-green taxa (Holton et al., 1964). Palmitic acid (16:0) occurred abundantly as had been noted in other studies (Chuecas and Riley, 1969; Ackman et al., 1970) and the high level of 14:0, although characteristic of diatoms (McIntire, Tinsley and Lowry, 1969), has been demonstrated for green algae on at least one other occasion (Lovern, 1936). Linolenic acid (18:3) seldom occurred in large amounts, an unusual feature as it is common in many different groups of algae. Comparably low levels have, however, been recorded by Chuecas and Riley (1969) for several marine species. Unsaturated C_{20} acids occurred in roughly the same proportion as that described for Cladophora and Oedogonium grown in the laboratory (Lovern, 1936). As with the phospholipids, changes in the proportion of 16:0 and 18:1,as well as that of 16:1,bore little resemblance to the pattern of change predicted from laboratory studies, again reflecting the affect of many environmental factors on the algae.

5. The Role of Algae in the Diet of *Asellus aquaticus* L. and *Gammarus pulex* L.

Introduction

The food of *Asellus aquaticus* L. and *Gammarus pulex* L. consists of a variety of different materials including decaying vegetation, microscopic algae and invertebrates. On the basis of the gut contents of these and related species, several workers have concluded, however, that the most important food in the diet is allochthonous leaf material (Haempel, 1908; Willer, 1922; Steusloff, 1943; Levanidov, 1949; Hynes, 1954, 1963; Minckley, 1963; Minshall, 1967). Furthermore, the rearing of *Asellus* or *Gammarus* on a diet of decaying leaves indicated that the animals feeding on this food source utilized the epiphytic fungi and bacteria on the leaves (Hynes and Williams, 1965; Kaushik and Hynes, 1971; Prus, 1971, 1972; Bärlocher and Kendrick, 1973a,b; Nilsson, 1974). Although the other components of the diet have usually been ignored, Margalef (1948) has reported that *G. pulex* fed chiefly on insects and copepods, and Deksbakh and Sokolova (1965) have stated that *G. lacustris* Sars relied mainly on algae, macrophytes and invertebrate animals.

Since most of the information on invertebrate feeding is qualitative (Hynes, 1970), serious errors may exist in the estimation of the relative importance of the different dietary components. As the algal fraction has been relatively neglected, this quantitative study has investigated its role in the diet of *A. aquaticus* and *G. pulex* collected from different rivers.

Methods

Thirty to forty individuals of Asellus and Gammarus were collected by hand at two weekly intervals between June 1973 and May 1974. The samples, taken from rocks and from growths of Cladophora glomerata in the River Wylye, Wellow Brook and the Kennett and Avon Canal, were immediately preserved in Transeau's solution (Prescott, 1962). The stomach and the anterior end of the mid gut (Hynes, 1954) were dissected out in the laboratory and a wet mount prepared of the contents. Algae other than diatoms were identified and enumerated at a magnification of 400 times. The entire sample was then cleared in concentrated nitric acid and fixed in Clearax mountant to permit identification and enumeration of the ingested diatoms at a magnification of 1000 times. By using the procedure of Moore and Beamish (1973) it was found that a count of 100 algal cells per individual would provide an accurate estimate of the stomach contents. The data obtained from the above analyses were then compared with the relative abundance of the flora described earlier in Section 2.

The guts of 25 - 30 specimens of each species were dissected out on several occasions during the study and the relative abundance of diatoms determined. After oxidation of each sample in 5-10 ml concentrated nitric acid, three 65 μ l aliquots were taken and all the diatoms in the individual aliquots enumerated. From these data it was possible to estimate the total number of algae in each animal. The cell counts were then converted into cell volume as previously described on page 6.

The density of A. aquaticus and G. pulex longer than 5 mm in the Wylye during August and December was estimated from collections made by hand over an area of 2 m^2. A plankton net was held immediately downstream from the collection area to ensure the capture of any dislodged and drifting organisms. Collections were also made in the Kennett and Avon Canal during January and March. These animals were picked by hand from three 10-15 g (wet weight) samples of Cladophora collected under water in a plastic container.

The rate at which food evacuated from the gut of both A. aquaticus and G. pulex was determined at 15°C (range 14.5 - 15.5°C) and 5°C (range 4.5 - 5.5°C) for 20 animals of each species 8 - 15 mm in length. For these experiments, samples were collected from Wellow Brook during the summer and winter at times when the water temperatures in the field approximated those of the experimental regime. When the animals had been held at their acclimation temperature for 14 days and allowed to feed freely on algae and decaying leaves, they were then placed among stones in water that contained no food. After the ingested material had passed to the posterior end of the gut, a process that could be easily observed under the microscope, further samples were taken for dissection purposes to determine the precise time taken for evacuation.

Utilization of Algae

River Wylye

Diatoms were the most common type of algae ingested by both Asellus aquaticus and Gammarus pulex in the River Wylye, always accounting for at least 80% of the ingested flora. The forms most frequently consumed by both animals during the spring were Achnanthes lanceolata, Nitzschia palea and N. linearis while, in the summer and autumn, the most important species were Achnanthes minutissima and N. palea. At other times of the year, A. minutissima, Cymbella affinis and varieties of C. ventricosa were of major significance. Green and blue-green algae were always ingested in relatively small amounts and the total of these two taxa never accounted for more than 20% of the intestinal contents. In most instances, the relative abundance of the algal species in the stomachs of both animals was similar to that recorded from the environment, a feature exemplified by the December data (Fig. 64) A notable exception was observed during August, however, when the blue-green algae Phormidium foveolarum was ingested in disproportionately small numbers while the opposite pattern was observed for several diatom species (Fig. 65).

Usually, the species composition of the gut contents of both A. aquaticus and G. pulex did not change with the size of the animal, as can be seen in the December data (Table 27). Furthermore, the mean length of ingested algae was also the same regardless of size of animal. For example, during December, the average cell size in samples of A. aquaticus shorter than 6 mm was 26.7 µm. Similarly, the algae ingested by G. pulex on the same data averaged 25.6 µm in specimens shorter than 6 mm and 25.4 µm in those longer than 12 mm.

The longest diatom found in the gut of both A. aquaticus and G. pulex was Synedra ulna. Normally only fragments of this species were seen in the stomach although specimens shorter than 110 - 130 µm often remained intact. The longest blue-green alga ingested by the animals was Phormidium foveolarum. Its maximum length in the stomach averaged 250 - 300 µm in both species and, in most instances, the filaments appeared to be entire. The diatom Achnanthes minutissima, averaging 10.5 µm in length (range 7.0 - 21.1 µm), was the smallest alga commonly ingested by both animals.

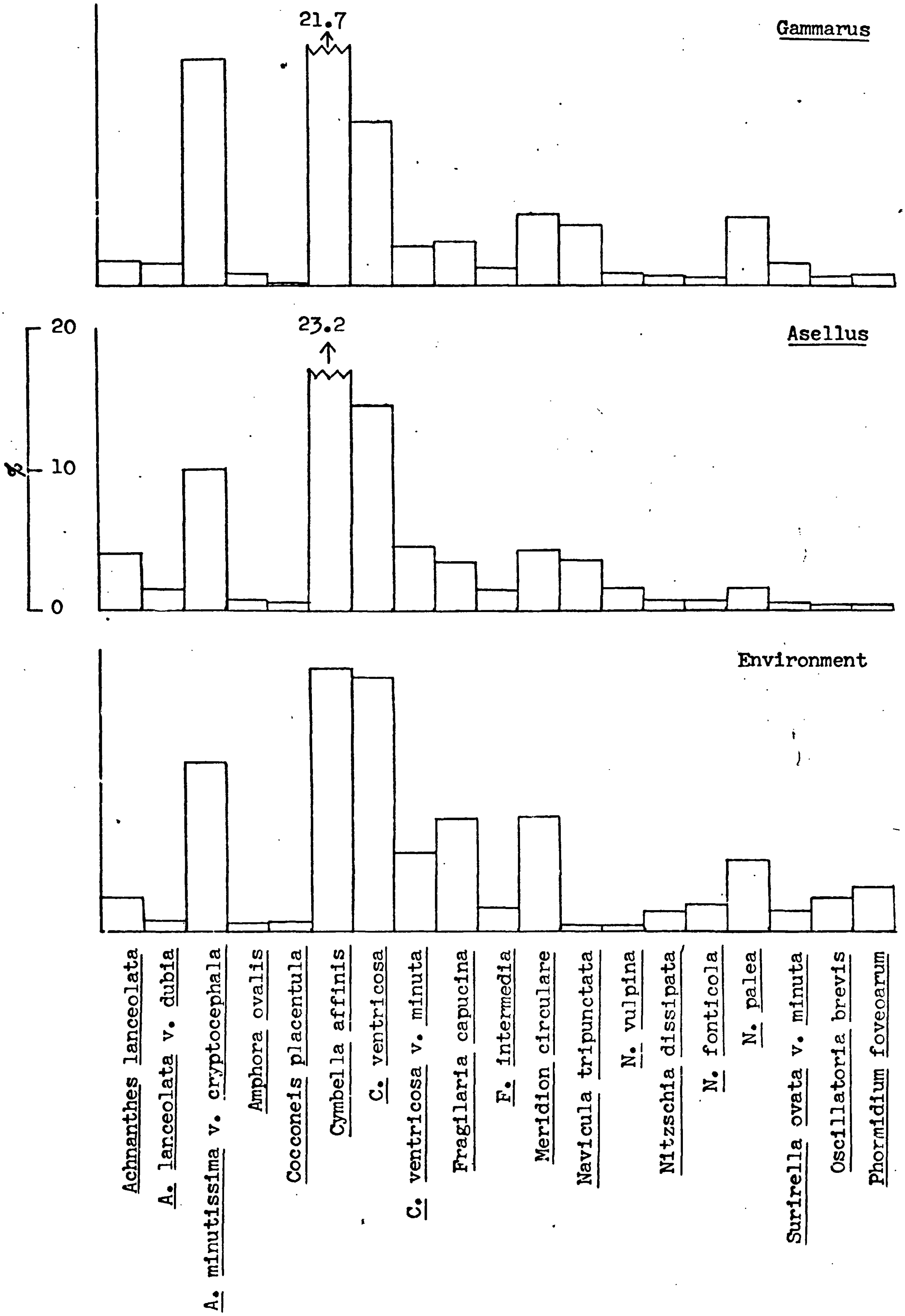

Fig. 64. Mean relative abundance of dominant algae during December 1973 associated with rocks in the River Wylye together with their mean relative abundance in the stomachs of Asellus aquaticus and Gammarus pulex.

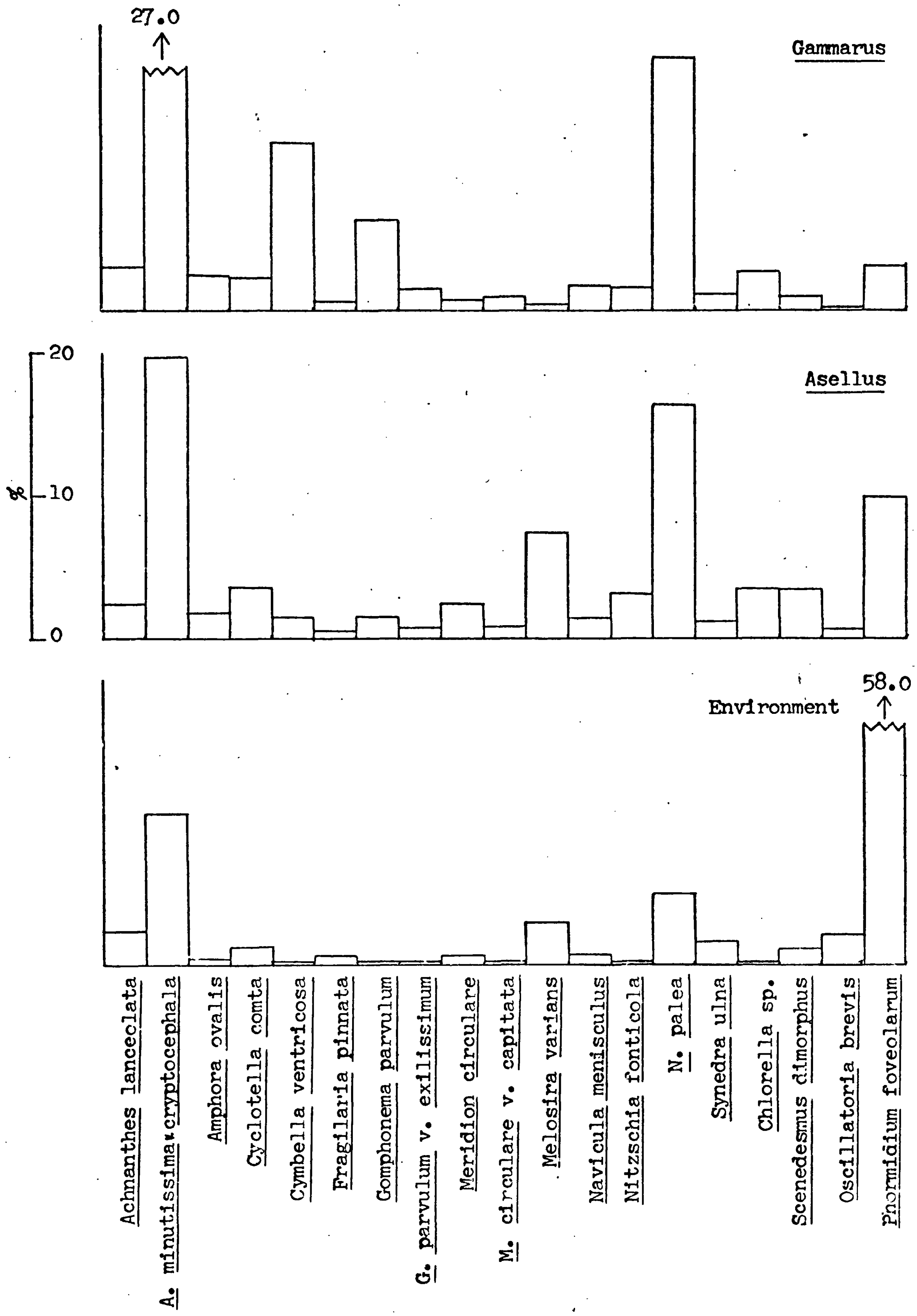

Fig. 65. Mean relative abundance of dominant algae during August 1973 associated with rocks in the River Wylye together with their mean relative abundance in the stomachs of Asellus aquaticus and Gammarus pulex.

Table 27. Mean (± 1 SD) expressed as a percentage by numbers of dominant algae in the stomachs of *Asellus aquaticus* and *Gammarus pulex* in the River Wylye during December 1973 and the Kennett and Avon Canal during March 1974.

River Wylye

Asellus aquaticus

Length Class (mm)	*Achnanthes lanceolata* and varieties	*Achnanthes minutissima*	*Cymbella affinis*	*Cymbella ventricosa*	*Cymbella ventricosa* v. *minuta*	*Meridion circulare*
6	4.3 ± 0.9	9.1 ± 2.9	25.6 ± 5.1	12.2 ± 2.9	5.1 ± 0.9	5.0 ± 0.9
6 - 9	4.8 ± 1.7	12.3 ± 2.8	20.3 ± 4.1	15.0 ± 3.1	4.5 ± 2.1	4.1 ± 0.5
9 - 12	6.1 ± 1.7	10.0 ± 3.1	19.6 ± 3.6	14.8 ± 3.3	4.0 ± 1.0	3.7 ± 0.6
12	6.8 ± 1.3	8.6 ± 2.8	27.3 ± 2.8	18.0 ± 2.9	4.4 ± 1.8	4.0 ± 1.1

Gammarus pulex

Length Class (mm)	*Achnanthes lanceolata* and varieties	*Achnanthes minutissima*	*Cymbella affinis*	*Cymbella ventricosa*	*Cymbella ventricosa* v. *minuta*	*Meridion circulare*
6	2.5 ± 1.1	16.3 ± 4.1	23.2 ± 5.1	13.3 ± 2.7	1.9 ± 0.5	5.3 ± 1.1
6 - 9	3.3 ± 1.2	14.9 ± 3.1	19.7 ± 4.3	12.8 ± 1.9	2.6 ± 0.4	4.7 ± 1.0
9 - 12	4.0 ± 1.4	17.9 ± 3.9	20.6 ± 2.6	9.7 ± 3.4	2.8 ± 0.8	4.7 ± 0.9
12	2.2 ± 1.0	14.9 ± 2.9	23.3 ± 3.1	11.0 ± 2.6	2.7 ± 0.5	5.3 ± 1.3

Table 27. (cont'd).

Kennett and Avon Canal

Asellus aquaticus

Length Class (mm)	*Achnanthes minutissima*	*Gomphonema olivaceum*	*Gomphonema subclavatum*	*Navicula vulpina*	*Nitzschia subtilis* v. *paleacea*	*Oscillatoria angustissima*
6	47.1 ± 4.9	5.3 ± 1.8	9.8 ± 4.6	14.0 ± 3.1	1.3 ± 0.2	6.5 ± 1.7
6 - 9	51.5 ± 6.2	5.3 ± 1.9	10.5 ± 2.7	13.8 ± 1.9	1.1 ± 0.2	7.9 ± 1.9
9 - 12	53.2 ± 4.3	4.3 ± 2.4	15.8 ± 3.6	15.6 ± 2.8	1.1 ± 0.2	7.0 ± 1.4
12	45.8 ± 5.6	5.1 ± 0.9	13.9 ± 4.1	13.8 ± 2.2	1.7 ± 0.3	6.6 ± 1.3

Gammarus pulex

Length Class (mm)	*Achnanthes minutissima*	*Gomphonema olivaceum*	*Gomphonema subclavatum*	*Navicula vulpina*	*Nitzschia subtilis* v. *paleacea*	*Oscillatoria angustissima*
6	46.2 ± 4.6	5.1 ± 1.8	11.3 ± 3.3	11.6 ± 2.6	4.8 ± 1.7	3.4 ± 0.9
6 - 9	48.0 ± 6.7	4.7 ± 1.7	11.0 ± 3.9	12.3 ± 2.8	3.2 ± 0.9	3.5 ± 1.3
9 - 12	43.1 ± 5.1	4.7 ± 1.1	9.2 ± 4.4	15.0 ± 3.1	3.9 ± 1.1	4.2 ± 1.7
12	39.5 ± 9.6	5.5 ± 1.4	10.5 ± 3.8	15.1 ± 2.9	4.1 ± 1.4	4.1 ± 1.2

The total volume of algae found in the gut of Asellus aquaticus decreased on a unit weight basis with size (Fig. 66). During August, for example, specimens weighing 80 mg contained about 30×10^6 μm^3 of algae while those of 3 mg contained only about 3.1×10^6 μm^3. The pattern of change during December was similar to that observed in August but values were much lower, i.e. 3.5×10^6 and 0.5×10^6 μm^3 respectively. A similar trend was observed in Gammarus pulex, although, as illustrated in Fig. 66 , this animal invariably had less algae in its gut than comparable specimens of A. aquaticus. For example, 80 mg individuals contained on the average 17×10^6 μm^3 of algae in the summer and 3.2×10^6 μm^3 in the winter.

Considerable quantities of sand grains and plant detritus were found with the algae in the gut of both animals but the relative importance of these components was not estimated.

Kennett and Avon Canal

The algae found in the stomachs of Asellus aquaticus and Gammarus pulex living among growths of Cladophora glomerata in the Kennett and Avon Canal again consisted mainly of diatoms. Achnanthes minutissima was the most frequently ingested species throughout the year, usually followed in much reduced numbers by Gomphonema and Navicula spp. Green and blue-green algae always formed a minor part of the diet, the two together never accounting for more than 10% of the ingested flora by numbers. The relative abundance of the algae found in the stomachs of both animals was generally similar to that recorded for the algae growing in association with Cladophora glomerata , but during the spring the proportion of ingested algae often bore little resemblance to that found in the environment. During March, for example (Fig. 67), Oscillatoria brevis accounted for 51.0% by numbers of the microscopic flora associated with Cladophora whereas it represented only 0.5 - 15.5% of the gut contents of the two species. Similarly, there were several instances in which certain algal taxa were ingested in disproportionately large numbers, the most notable example being Achnanthes minutissima which represented 18.1% of the assemblage in the environment and 44.2 - 49.4% of the stomach contents.

Typically, the species composition of the stomach contents of Asellus aquaticus closely resembled that of Gammarus pulex irrespective of the length of the animal (Table 27). Furthermore, the average

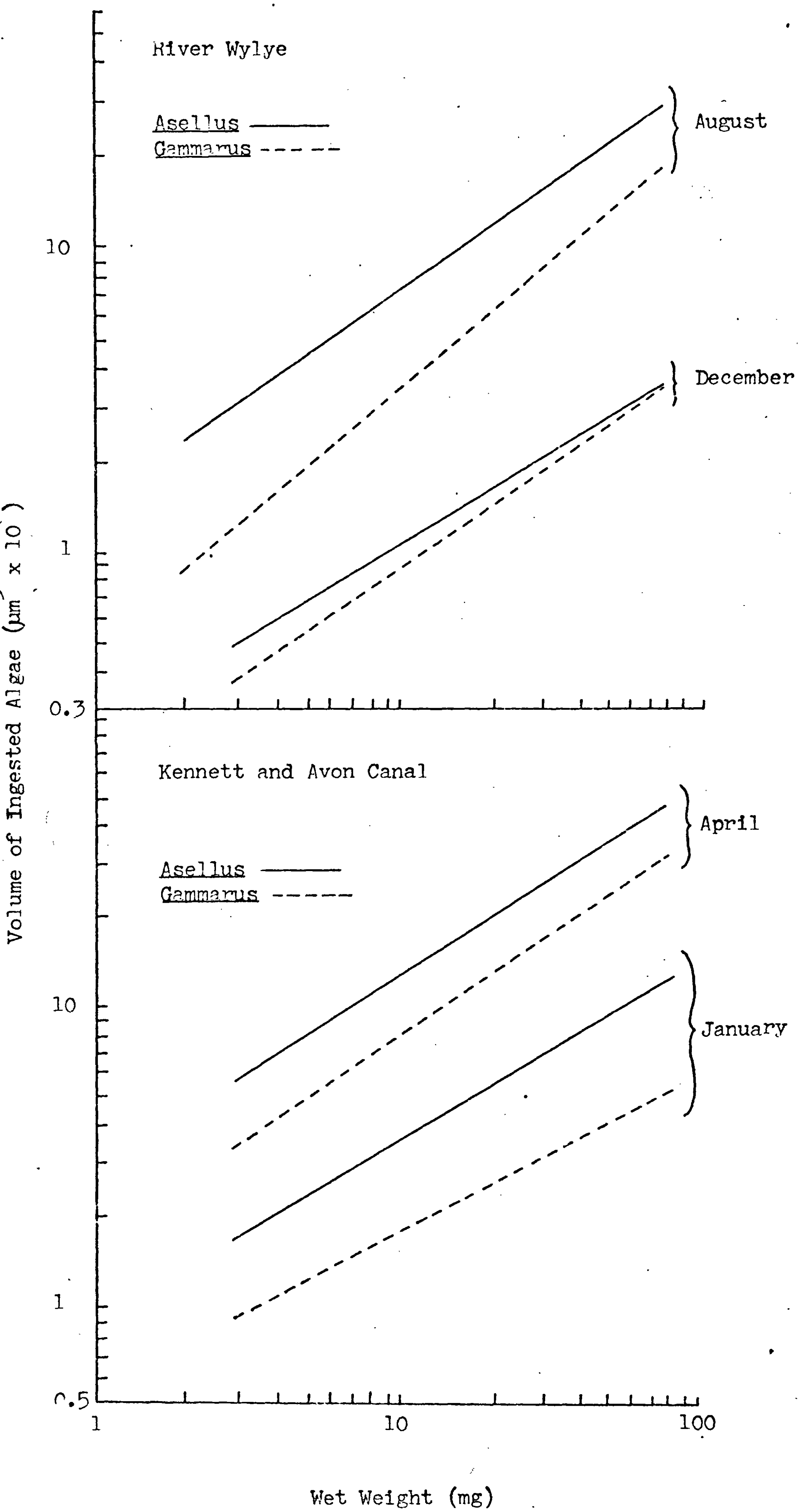

Fig. 66. Volume of algae in the gut of Asellus aquaticus and Gammarus pulex of different weight collected from the River Wylye during August and December 1973 and the Kennett and Avon Canal during January and April 1974.

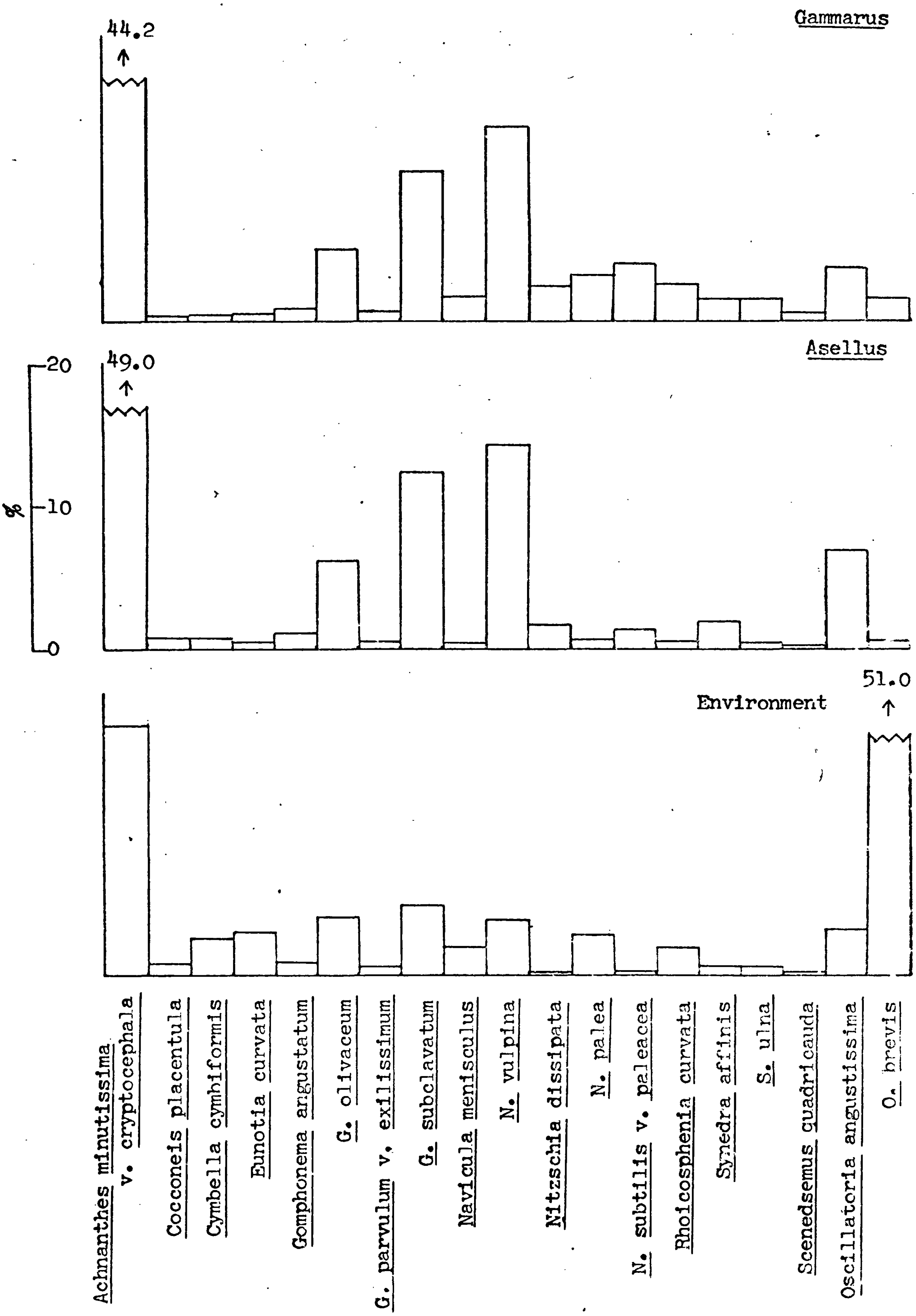

Fig. 67. Mean relative abundance of dominant algae during March 1974 associated with Cladophora glomerata in the Kennett and Avon Canal together with their mean relative abundance in the stomachs of Asellus aquaticus and Gammarus pulex.

size of ingested cell was the same regardless of species or size. For example, specimens of Asellus aquaticus shorter than 6 mm contained particles that averaged 34.5 µm in length during March while the corresponding value for representatives of Gammarus pulex greater than 12 mm was 31.5 µm.

The longest diatom species ingested by both A. aquaticus and G. pulex was Synedra ulna v. amphirhynchus, but once again only those cells shorter than 120 - 140 µm were left intact. On the other hand, apparently entire filaments of the blue-green alga, Oscillatoria angustissima, measuring 300 µm in length were frequently found among the stomach contents. The smallest algal species often ingested by the two animals, Achnanthes minutissima, measured 6.3 to 22.7 µm in length.

The total volume of algae in the gut of Asellus aquaticus was considerably greater than that of specimens collected from rocks in the River Wylye. For example, 80 mg animals normally contained $14 \times 10^6 \mu m^3$ of algae in January and $47 \times 10^6 \mu m^3$ in April (Fig. 66). Similarly, the algal content of 80 mg specimens of G. pulex averaged 5 and $32 \times 10^6 \mu m$ respectively.

Considerable amounts of sand and plant detritus were found in the gut of both animals but once again their importance was not estimated. Fragments of Cladophora never appeared in the stomach contents.

Wellow Brook

Diatoms always accounted in Wellow Brook for at least 95% of the algal flora ingested by those Asellus aquaticus and Gammarus pulex which were living among growths of Cladophora glomerata. Rhoicosphenia curvata was invariably the most common species found in the gut, seldom accounting for less than 30% of the ingested flora of both animals. Other important species included filamentous taxa, e.g. Diatoma vulgare Bory and Melosira varians, as well as Navicula spp. In many instances the relative abundance of ingested algae bore little resemblance to that found in the environment, a point well illustrated by the October data (Fig. 68). During this period, Cocconeis pediculus, C. placentula v. euglypta and Lyngbya sp. were rarely eaten even though they occurred commonly in association with Cladophora whereas several other diatom species

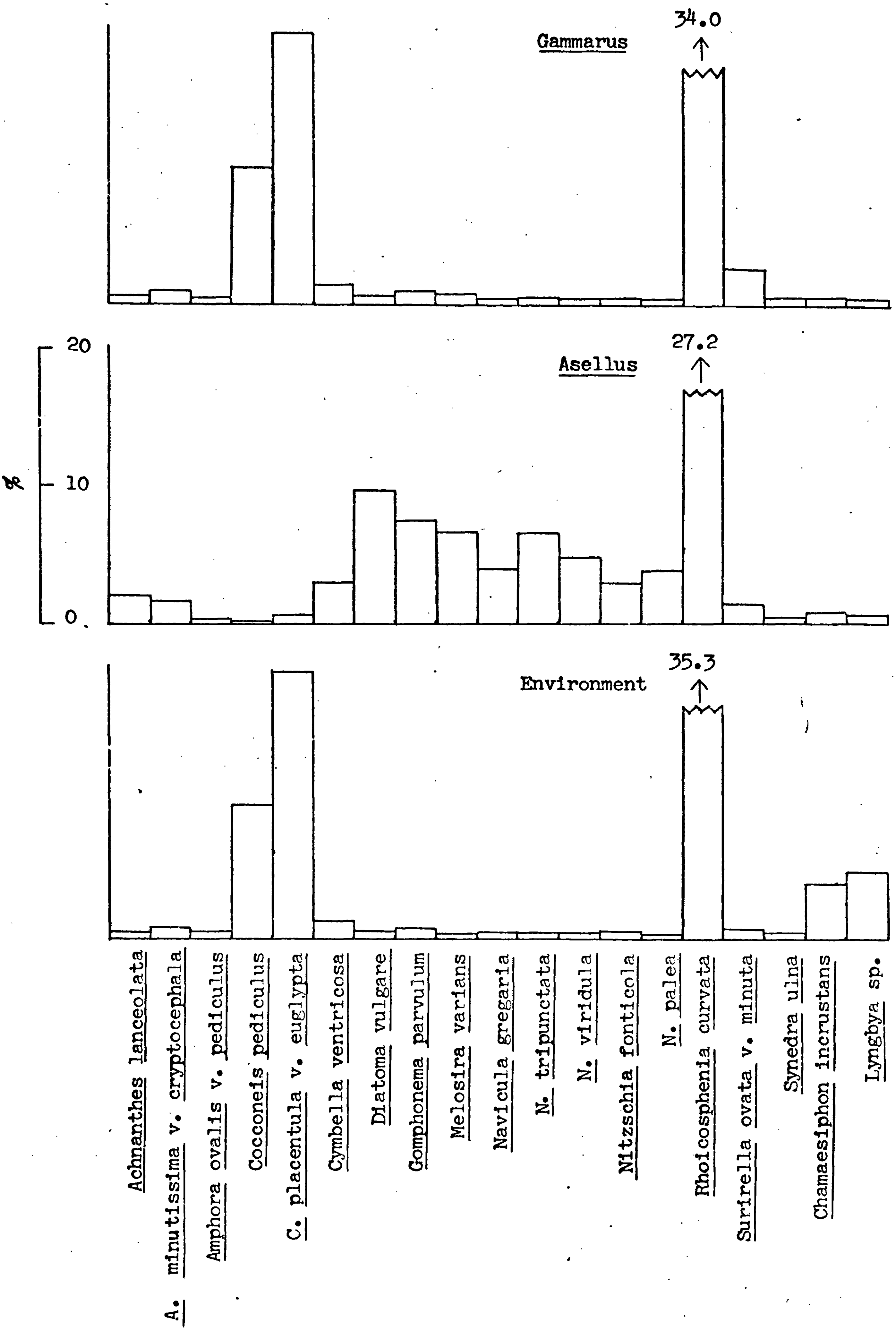

Fig. 68. Mean relative abundance of dominant algae during October 1973 associated with Cladophora glomerata in Wellow Brook together with their mean relative abundance in the stomachs of Asellus aquaticus and Gammarus pulex.

were ingested in disproportionately large quantities. Other aspects of the utilization of algae in Wellow Brook were virtually identical to those described for animals living in the Kennett and Avon Canal.

Digestion, Evacuation and Grazing

The cell wall of all the ingested algae normally appeared intact regardless of species of animal or season. However, as mentioned earlier, entire diatom cells longer than 120 -140 μm (e.g. Synedra ulna and varieties) never occurred in the stomachs although blue-green forms of comparable length were left intact. A considerable amount of algae which had retained the colour of their chloroplast occurred near the posterior region of the gut of both animals. In the River Wylye during December, for example, 44% of the specimens of Cymbella affinis ingested by Asellus possessed intact chloroplasts while the corresponding value for Gammarus was 66% (Table 28). Virtually all those algal species retaining the colour of their chloroplasts were able to survive and reproduce in Rodhe 8 medium (Rodhe, 1948).

Complete emptying of the gut of Asellus aquaticus took 25 h (range 22 - 30 h) at 15°C and 75 h (range 70 - 85 h) at 5°C. Gammarus pulex, on the other hand, required 18 h (range 16 - 20 h) at the higher temperature and 40 h (range 35 - 47 h) at the lower. The amount of algae ingested daily by the two animals was calculated from the relation between the quantity of algae in their guts and the rate of emptying. Thus, during the summer, for example, an 80 mg A. aquaticus in the River Wylye ingested approximately 28.8×10^6 μm^3 of algae while those of 3 mg consumed about 3.0×10^6 μm^3 each day. On the other hand, 80 mg specimens of G.pulex ingested 22.6×10^6 μm^3 of algae daily while the corresponding value for 3 mg individuals was 1.7×10^6 μm^3. These calculated values are based on the assumption that the number of algal cells in the gut remained constant over each 24 h period. This point was verified by counts of all the algae in 10 - 15 representatives of each species collected once every two months at 4 h intervals. The results, based on samples from both the River Wylye and the Kennett and Avon Canal showed no consistent pattern of diurnal variation in numbers and there was never more than a 10% difference between comparable collections.

The average density of A. aquaticus over the collection area in the River Wylye was estimated at approximately 20 individuals m^{-2} during December and 55 m^{-2} during August. The average weight of these specimens was 40 mg regardless of season. Thus, approximately 0.75 x

Table 28. Percentage of algae found in the posterior end of the gut of *Asellus aquaticus* and *Gammarus pulex* collected from the River Wylye which had retained the colour of their chloroplast. The number of animals examined in each species was 30 per sampling date.

Taxon	August		December	
	A. aquaticus	*G. pulex*	*A. aquaticus*	*G. pulex*
Achnanthes minutissima	1.5	9.0	13.9	15.3
Cymbella affinis	18.7	20.1	44.1	66.0
Cymbella ventricosa	23.3	30.1	17.8	37.4
Meridion circulare	25.1	23.6	10.7	15.3
Nitzschia palea	5.2	10.3	29.0	18.1

10^6 μm^3 of algae would be ingested per day during December by animals weighing 40 mg , a value which by extrapolation gives a consumption of 15.0×10^6 μm^3 for the population living in one m^2 of river bed. During August the corresponding values would increase to 0.019×10^6 and $1.0^3 \times 10^9$ μm^3 , respectively. The average density of Gammarus over the same collection site was estimated in December at about 80 and in August as 110 individuals m^{-2} with corresponding average weights being about 20 and 30 mg. Some 61.6×10^6 μm^3 of algae would thus be ingested per m^2 per day in the winter while the corresponding value for the summer population would be about 1.2×10^9 μm^3.

Approximately six representatives of Asellus, averaging 24 mg in weight, were found per g dry weight of Cladophora in the Kennett and Avon Canal during April, thus implying that about 0.13×10^9 μm^3 of algae were ingested daily by this population. Similarly, in the winter , the density of the animals averaged 18 g^{-1} and the mean weight of this collection was 35 mg giving a total daily consumption of 45.4×10^6 μm^3 g^{-1} . Since Gammarus was present at densities of approximately 4 individuals g^{-1} during April and their average weight was 15 mg , the total daily consumption of algae was 58.8×10^6 μm^3 g^{-1}. Likewise, in the winter, when there were 15 individuals g^{-1} whose average weight was 20 mg, the population at this time would consume 23.0×10^6 μm^3 g^{-1} day^{-1}.

The amount of algae on the rocks in the River Wylye fluctuated considerably during the study but normally ranged from 1.0 – 5.0 $\times 10^9$ μm^3 cm^{-2}. During the spring, however, values rose to 10 – 13 $\times 10^9$ μm^3 cm^{-2} while the lowest standing crop , 0.2×10^9 μm^3 cm^{-2}, was observed briefly during the winter. The amount of algae associated with Cladophora in the Kennett and Avon Canal remained at comparatively low levels, e.g. $5 \times 10^9 \mu m^3$ g^{-1} of Cladophora, during the autumn and most of the winter but values rose sharply in March to 45×10^9 μm^3 g^{-1} , tapering off to 20 – 30 $\times 10^9$ μm^3 g^{-1} for the remainder of the year. As all these values are considerably higher than the daily consumption figures mentioned above, it seems likely that grazing by both Asellus aquaticus and Gammarus pulex would not significantly effect the algal populations.

Discussion

One of the most striking features of this investigation is the high degree of selection exhibited for certain species by both Asellus aquaticus and Gammarus pulex. For example, filamentous blue-green forms and epiphytic Cocconeis spp. were rarely eaten whereas Achnanthes minutissima and several other diatoms were often ingested in disproportionately large quantities. The scarcity of Cocconeis spp. in the stomachs of animals living among the growths of Cladophora glomerata is probably attributable to the fact that they were the only adnate forms in the assemblage , their upper surface lying only 3 µm from the substrate. It is therefore likely that both animals were unable to dislodge particles so close to the filaments. In contrast, Melosira varians and Diatoma vulgare , the only diatoms forming long filaments on Cladophora, were ingested in disproportionately large quantities. Presumably, the majority of their cells were more accessible than those of almost all the other taxa which lie relatively close to the substrate. That Cladophora was never eaten is probably a reflection of the relative strength of its cell wall.

Although filamentous diatoms were frequently ingested, blue-green forms of comparable size were seldom eaten, suggesting that size selection was not responsible for their scarcity in the gut. As it also seems unlikely that the blue - green species would have been significantly more difficult to remove from the substrate than diatoms, it appears that both Asellus aquaticus and Gammarus pulex can select against at least certain forms of blue-green algae on a chemical basis, as is apparently the case for many other invertebrates (e.g. Gajevskaja, 1958). In the context of selection, it is worth noting that Kaushik and Hynes (1971) have reported that both Asellus and Gammarus demonstrate a preference for dead leaves of certain species which, in part, may be based on chemical stimuli.

Many species of algae appeared to be ingested in disproportionately large numbers on certain occasions but not on others. In those instances in which unusually large quantities appeared in the gut, other predominant forms were seldom eaten. This apparent selection for certain species is thus the result of a bias in the data, a point well illustrated by the August results for the River Wylye (Fig. 65).

in which many forms occurred much more frequently in the gut than on the rocks. If, however, the relative abundance of these taxa in the environment is calculated in the absence of Phormidium foveolarum, virtually all the data from both the gut contents and rocks are comparable.

The diet of both Asellus and Gammarus was similar irrespective of size, a situation contrasting with that reported by Brown (1960) for mayfly larvae where the species composition changed as the animal grew. However, it should be noted that in the latter study, both large filamentous algae as well as microscopic forms were present, whereas in the present investigation, nearly all of the predominant algae were of relatively similar length.

Considerable quantities of algae passed through the gut of both Asellus and Gammarus without apparent harm. Such a feature has been reported for many other animals including cladocerans (Le Fèvre, 1942), oysters (Loosanoff and Engle, 1947), lamellibranchs (Ballantine and Morton, 1956), larval lampreys (Moore and Beamish, 1973) and mayfly nymphs (Brown, 1960). Survival of the algae was always greater in winter than summer, probably reflecting the effect of low water temperatures on the digestive efficiency of the animals. Since Achnanthes minutissima had the lowest survival rate regardless of season, a pattern also noted for larval lampreys (Moore and Beamish, 1973), the cell wall of this taxon is presumably highly permeable to digestive enzymes. Asellus aquaticus appeared to digest most algal species better than Gammarus pulex, irrespective of season. The time required for the complete emptying of the gut of Asellus aquaticus and Gammarus pulex fell within the range normally reported for many aquatic animals including microphagous herbivores (Brown, 1961; Brett and Higgs, 1970; Beamish, 1972; Elliott, 1972; Goulder, 1972; Moore and Beamish, 1973). The fact that the food of Asellus aquaticus took longer to pass through the gut than was the case with G. pulex may well be correlated with its higher digestive efficiency.

Although considerable quantities of algae were ingested by the populations of A. aquaticus and G. pulex living in the two different habitats, the amount of algae in the environment was, however, always at least 10,000 times greater than that consumed by the animals per day, indicating that neither species had marked effect on algal numbers. Such a view is consistent with reports for other herbivores living in streams (e.g. lamprey larvae) although the contrary suggestion has also been made for the larvae of both the Trichoptera (Douglas, 1958) and Ephemeroptera (Brook, 1955b).

Since detritus was always found in the gut of both crustaceans, it was also presumably of nutritional importance. Unfortunately, as there was no precise way of determining the volume or weight of the ingested detritus, the importance of this component relative to algae could not be estimated. By comparing, however, the volume of ingested algae to the total volume of the gut contents, it is possible to determine the relative algal component in the diet of the animals. For a specimen of Asellus weighing 30 mg in the River Wylye during August, the total volume of the gut contents, estimated using a micrometer at 50 times, averaged 0.100 mm^3 (N = 15). From Fig. 66 animals of this size contained approximately 0.015 mm^3 of algae implying that this latter component accounted for 15.0% of the ingested material. During December, the volume of gut contents of animals of comparable size was 0.014 mm^3 and the amount of ingested algae was 0.002 mm^3, giving a value of 14.3%. As the total gut contents undoubtedly contained pockets filled with mucus, water and other material, both of these values must be considered conservative estimates. The volume of the gut contents of Gammarus during August averaged 0.234 mm^3 indicating that algae represented about 3.5% of the ingested material. The corresponding value in December, using 0.060 mm^3 as the average volume of the gut contents, was 3.00%, these values once again probably being conservative estimates. For specimens of A. aquaticus and G. pulex living among growths of Cladophora in the Kennett and Avon Canal, however, the relative volume of algae in the gut is 2 - 3 times greater than the values for animals from the River Wylye. This feature is directly attributable to the greater amount of microflora in their guts. While microscopic algae can thus be assumed to be a significant component of the diet of A. aquaticus and, to a lesser extent, in G. pulex, the degree of importance varies with habitat.

Unpublished data of the author on larval sea lampreys, Petromyzon marinus L., living on algae and detritus in streams tributary to Lake Ontario indicated that in a 1.0 g specimen the gut contents occupied a volume of 20 - 25 mm^3 in summer and 5 - 10 mm^3 in winter. The number and volume of ingested algae at these times were approximately 300,000 and 0.21 mm^3 and 70,000 and 0.06 mm^3 respectively (Moore and Beamish, 1973). Algae thus represented approximately 0.93% of the gut contents in the summer and 0.80% in the winter, considerably less than they do in either A. aquaticus or G. pulex.

The data presented in this investigation demonstrate that algae are a consistent and probably important part of the diet of Asellus aquaticus and, to a lesser degree, Gammarus pulex. This conclusion, which differs from that of other studies, reflects in part the shortcomings of gut contents analyses based purely on a qualitative assessment. Furthermore, since algae are much richer in terms of utilizable energy than a comparable weight of allochthonous leaf material, their importance in the diet is almost certainly considerably higher than would appear to be the case merely from their relative abundance in the gut.

6. A Laboratory Study on the Feeding of Larvae of the Brook Lamprey, *Lampetra planeri* (Bloch)

Introduction

The larval lamprey (ammocoete), a relatively sedentary animal living in burrows in the soft deposits of streams and rivers relies for food on the filtration of microscopic detritus and plant and animal organisms. The water current entering the pharyngeal chamber serves a nutritive as well as a respiratory function, the food particles being collected on mucous strands which are passed backwards to the intestine (Sterba, 1953, 1961). While some workers have recorded the presence of Protozoa, rotifers, nematodes and even small annelids in the gut (see Hardisty and Potter, 1971a) there can be little doubt that algae, and particularly diatoms, are much more frequently ingested (Creaser and Hann, 1929; Schroll, 1957, 1959; Alvarez del Villar, 1966; Moore, 1972; Potter, Cannon and Moore, In press). That algae are of nutritional value is demonstrated by the fact that the proportion of cells with colourless chloroplasts is significantly higher in the posterior region of the gut (Moore and Beamish, 1973). In this latter investigation of the feeding biology of the larvae of the landlocked and anadromous forms of the sea lamprey, *Petromyzon marinus* L., a relationship was shown to exist between the number of algal cells in the gut and both the size of the animal and the temperature of the water. It also demonstrated that, particularly in the winter, a considerable amount of detritus was ingested, an observation also made by Schroll (1959) in the case of the brook lampreys *Lampetra planeri* (Bloch) and *Eudontomyzon danfordi* Regan. Detritus, it should be noted, is regarded in this study as finely particulate decaying plant and animal material.

Although there is no information on the digestive efficiency of the ammocoete, the presence of large numbers of live algal cells in the hind end of the gut suggests that it is almost certainly low. Furthermore, the possibility cannot be excluded that, in addition to algae and detritus, bacteria and the organic substances dissolved in the water are also of significance as a food alone. The view that the latter two may be relevant is supported by the observation that relatively high densities of ammocoetes have been reported in places where there are decaying animal carcasses (Hardisty and Potter, 1971 a).

This paper reports experiments carried out in the laboratory to ascertain the extent to which, for the purpose growth, ammocoetes of the brook lamprey, Lampetra planeri, can utilize algae, detritus, bacteria and dissolved organic substances. Determinations have also been made of the assimilation efficiency of larvae fed exclusively on a diet of algae.

Materials and Methods

Ammocoetes of the brook lamprey, Lampetra planeri (Bloch), were collected during the summer of 1973 and the winter of 1974 by electrofishing in Highland Water. They were immediately transported to the laboratory and held for two weeks in 40 l tanks supplied with fine sand to a depth of approximately 15 cm. A photoperiod paralleling environmental conditions was adopted with a light intensity of 175 lux at the water surface. The temperature of the water was held at approximately the same level as that recorded in the field at the time of capture. Algae, mainly Chlorella sp., Cymbella affinis Kz., Nitzchia palea (Kz.) W.Sm., were added to the water and maintained at a concentration of 1-2 x 10^6 cells l^{-1}, comparable to that of the plankton in many of the rivers investigated during the summer. After a few days, algal numbers in the gut reached levels similar to those in natural populations of P. marinus (Moore and Beamish, 1973). After this initial acclimation period, the water in the tanks containing larvae caught in the winter was adjusted to 5.0°C (range 4-6°C), while that of larvae taken during the summer was changed to 15.0°C (range 14.5-15.5°C). Neither of the alterations to the new acclimation regime involved more than a 2°C change. The animals were held at these temperatures for an additional four weeks, maintaining the food, substrate and light conditions as before.

Detritus was collected from Highland Water by removing the uppermost 2-3 cm of sediment, swirling the sample in distilled water in the laboratory and letting the sand and heavy particles settle for two minutes. Algae, Protozoa, rotifers and other organisms were almost completely absent from the remaining material and, apart from a few spores, fungi were never observed. These observations on the paucity of the micro-fauna and flora in the detritus reflect their scarcity in Highland Water (page 23). To determine the growth of larvae fed solely on detritus, a group of 15 animals from the summer acclimation regime, i.e. 15°C, were weighed after light anaesthetization in MS 222 (Sandoz), and placed in tanks held at the same temperature, these differing, however, in that they contained only sand and sterilised water. The procedure was repeated for animals acclimated at 5°C. Detritus was added and maintained in suspension by artificially generated water currents at a concentration of 20-30 mg l^{-1}, a level comparable to that found in the study rivers (page 63). Two groups of 15 animals were also run at both 5 and 15°C under the conditions described immediately above, but with food being absent in one, while the other was provided with algae representative of local streams at a concentration of 1-2 x 10^6 cells l^{-1}. The weight change of larvae fed solely on the bacterium Escherichia coli (Migula) was determined at four different concentrations (1 x 10^5, 1 x 10^6, 1 x 10^7, 1 x 10^8 cells ml^{-1}) using the same procedures. In all the above experiments the water was changed every four days and, where applicable, either detritus or organisms added at the relevant concentration. The collective wet weight of the 15 animals in each experiment was then recorded at the end of both 30 and 60 days and the value expressed as either a percentage loss or gain in weight compared with that recorded at the commencement of the experiment (Fig. 69).

In the first set of experiments with dissolved organic substances, glucose was maintained in two separate concentrations (1.0 and 5.0 g l^{-1}), the amino acids being added to each tank at a total concentration of 0.5 g l^{-1} in the proportions given in Table 29 while vitamins and minerals were maintained at 0.05 g l^{-1} in the proportions given by Mertz (1972). Only a small amount of the fatty acids, added at 0.5 g l^{-1} (Table 29), went into solution. The water in the tanks was changed every two days and sodium azide added to restrict bacterial growth. In the second set of experiments, the amino acids were kept at a concentration of 1.0 g l^{-1} while glucose and fatty acids were maintained at 0.5 g l^{-1} and the vitamins at 0.05 g l^{-1}. At higher amino acid concentrations, the ammocoetes died within a few days, possibly due to the excessively high nitrogenous levels produced.

Determinations of the proximate body composition were made of a group of 10 control animals at the commencement of the experiment and also for all animals at the end of each 60 day experimental regime. Lipids were extracted in chloroform: methanol as outlined on page 70 , while total protein was determined by the method of Fels and Veatch (1959). Ash was obtained by placing the material for 24 h in a muffle furnace at 550°C. These methods,

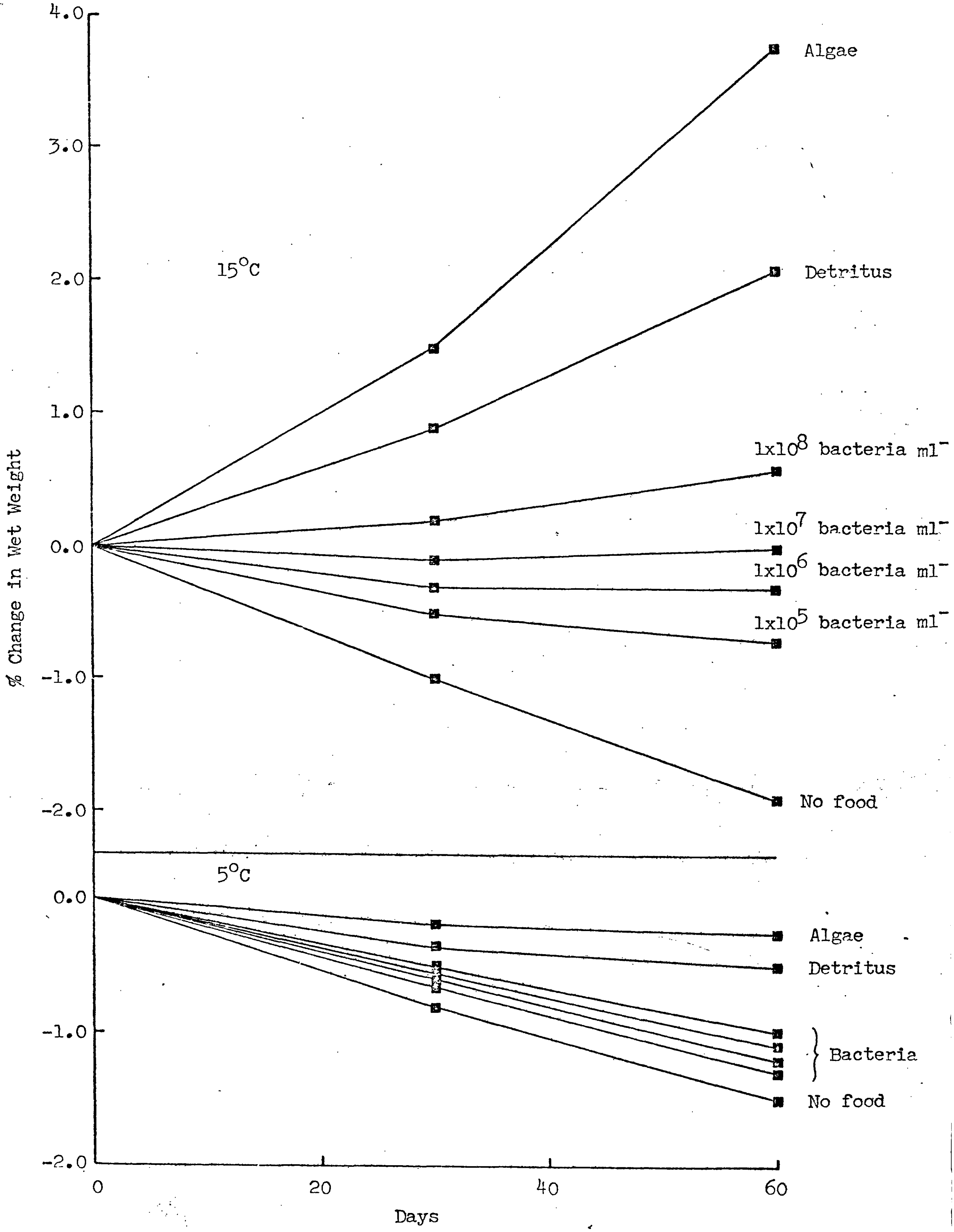

Fig. 69. The percentage change in weight of ammocoetes provided with several different food sources at 5 and 15°C.

Table 29

The percentage composition by weight of amino and fatty acids used in the experiments with dissolved organic substances.

Amino acid	
L - Glutamic acid	10.0
Glycine	10.0
L - Isoleucine	8.3
L - Leucine	8.3
L - Argenine.HCl	6.7
L - Aspartic acid	6.7
L - Lycine.HCl	6.7
L - Proline	6.7
L - Alanine	5.0
L - Threonine	5.0
L - Tyrosine	5.0
L - Valine	5.0
L - Histidine.HCl.H_2O	3.3
L - Methionine	3.3
L - Phenylalanine	3.3
L - Serine	3.3
L - Cystine	1.7
L - Tryptophan	1.7

Fatty Acid	
Oleic acid	30.0
Lineolenic acid	30.0
Palmitic acid	15.0
Stearic acid	8.0
Palmitoleic acid	5.0
polyunsaturated C_{20} acids	5.0
polyunsaturated C_{22} acids	5.0
Myristic acid	2.0

together with that of Updergraff (1969) for cellulose, were also used to ascertain the relative amounts of these components in the algae, detritus and bacteria used in this study (Table 30).

Ideally, estimates of assimilation efficiency (Prus, 1971) are carried out by comparing the chemical composition of the faeces with that of the food prior to its ingestion. Since, however, ammocoetes almost certainly take food from the water, the substrate and from within the substrate itself, it would be virtually impossible to isolate a representative sample of the ingested material. For this reason, the faeces composition was compared in this study with that found in the anterior 10% of the intestine's length using the insoluble fraction as a marker.

The tanks holding the animals for the assimilation studies were maintained at either 5 or 15°C and provided with algae at 1-2 x 10^6 cells l^{-1} in the manner already described. For each sample, 30 animals were quickly transferred to one l beakers containing a substrate of glass beads (0.5 - 1.0 mm) into which it was known that the ammocoetes would rapidly burrow and settle down (Hill and Potter, 1970; Potter and Rogers, 1972). After two hours, the lampreys were removed and the faeces collected by filtering the contents of the water through a Millipore membrane (0.45 µm). This experimental procedure was repeated six times at weekly intervals at 15°C but only once at 5°C where much lower values were obtained. Values for lipid, protein and cellulose were obtained as previously described. After the material had been ashed for 24 h at 550°C , the insoluble portion of the material was determined by extracting the soluble fraction in 50% HCl , the latter procedure being achieved within 10 minutes.

Prus (1971) has suggested that ash ratio methods, such as those described by Conover (1966), provide unreliable estimates for assimilation efficiencies. He based this view on the fact that as the ash contains both a soluble and an insoluble fraction, the former may be absorbed and excreted. In fact, he considers that the variation he obtained in his results for assimilation efficiencies in Asellus aquaticus using ash ratio techniques may be attributable to this phenomenon. Since, however, in the present study, only the insoluble fraction was considered and this contained mainly sand grains unlikely to alter in their passage through the gut, the ash component would appear to provide an ideal marker for ash ratio determinations of assimilation efficiency.

Table 30

Range in percentage chemical composition of algae, detritus and bacteria used in the various experimental regimes.

	Lipid	Protein	Carbohydrate	Cellulose	Ash
Algae	21–23	12–14	19–21	3–5	39–41
Detritus	2–3	1.5–2	28–33	7–9	55–65
Bacteria	20–22	63–67	5–6	0	8–9

at summer temperatures. Detritus has been shown to be ingested in large quantities by a wide range of other animals, including insect larvae (Slack, 1936; Moon, 1938; Jones, 1950; Brown, 1961; Chapman and Demory, 1963), molluscs (Boycott, 1936; Jørgensen, 1949) and crustaceans (Hynes, 1954; Steusloff, 1943; Levanidov, 1949). Although some species can use this material as an energy source (Hynes, 1970), it may be of considerably less importance for others (Slack, 1936).

The fact that at 15°C ammocoetes gained weight less rapidly when provided with detritus, as opposed to algae, almost certainly reflects the relative difference in the lipid, protein and carbohydrate content of the respective food sources (Table 30). It should be noted that since in this study the detritus was renewed frequently from collections made in Highland Water, its chemical composition was therefore the same throughout the experimental period as that found in the animal's natural environment. In addition, the ash levels in the detritus, although high (Table 30), were almost identical to those of ingested matter found throughout the year in the anterior part of the gut of larvae collected from Highland Water. Another probable product of the relative food quality of algae and detritus is shown by the length/weight relationship of animals taken from regions of relatively low and high level algal densities. A Condition Factor of 1.93 was calculated from regression equations for an animal of 1 g weight in May in Highland Water where the flora was not very abundant and the gut contained mainly detritus and, irrespective of season, less than 8000 algal cells. On the other hand, in the River Chew (Lat. 51°18' , Long. 2°36'), a much more productive algal source, animals of comparable weight at the same time of the year had a Condition Factor of 2.48 and contained more than 1×10^6 cells. Since neither detritus nor algae could support growth at 5°C , low water temperatures presumably effect the digestive efficiency of larval lampreys. This suggestion is borne out by the analysis of the proportion of live and dead cells in the posterior end of the gut of P. marinus caught in the summer and winter (Moore and Beamish, 1973). The reduced digestive efficiency, together with the far lower metabolic rate of ammocoetes at winter temperatures (Hill and Potter, 1970), are undoubtedly major factors

Results and Discussion

The ammocoetes used for all the experiments weighed between 0.85 and 1.15 g. In the case of animals fed at 15°C on either algae or detritus, a clear increase in the wet weight was observed between the first day and day 30 and between the latter and the completion of the experiment (Fig 69). The percentage increase over 60 days was greater, however, for animals fed on the living plant material (3.8%) than on detritus (2.1%). This is despite the fact that the organic dry weight of the gut contents of the larvae, expressed as a percentage of the wet body weight, was 0.2% in both cases. By contrast, animals provided with algae and detritus at 5°C decreased in weight by 0.25 and 0.50% respectively. At 15°C, animals provided with bacteria at a concentration of 1×10^8 cells ml^{-1} increased in weight by 0.6% while at 1×10^7 cells ml^{-1} they showed effectively no weight change. The organic dry weight of the gut contents of these two groups averaged only 0.05%. At lower bacterial concentrations the animals lost weight as they also did at all concentrations at 5°C. Animals provided with no food showed a weight decrease of 1.9% at 15°C and 1.5% at 5°C. Glucose and amino acids, and the limited supply of fatty acids which dissolved in the water, failed to support growth, irrespective of concentration or the temperature of the water. The pattern of weight change in each case followed closely that of the starved animals (Fig 69).

No significant difference was observed in any of the experimental regimes between the proximate body composition of the ammocoetes at the beginning and end of each of the experimental periods. The water content represented 71.5% (range 68.0 - 73.8) of the wet body weight while the corresponding percentages for lipid, ash and protein were 10.0 (7.5 - 13.2), 0.9 (0.8 - 1.0) and 16.0 (14.9 - 16.9) respectively. The absence of any change in the mean proximate body composition of animals examined just prior to the start of an experiment and those at the end of the experimental regimes may not, however, portray the situation occurring within each individual animal. It could, for example, reflect the variability found both in the field (Hardisty, 1961) and in animals held in the laboratory even under identical acclimation regimes.

It is clear from these results that detritus can act as a sufficiently nutritive food source to enable growth to take place responsible for the highly seasonal pattern of growth found in larval lampreys (Thomas, 1962; Potter, 1970; Lowe, Beamish and Potter, 1973).

In any consideration of the role of detritus in the diet, it is difficult to differentiate between the contribution made by the material itself and that of the microorganisms, such as bacteria and fungi, contributing to its decomposition. It has been demonstrated that some animals feed heavily on the fungi on leaf litter (Hynes et al., 1974) and bacteria have been shown to be a major energy source for many organisms, including crustaceans (Husson, 1962; Marzoff, 1965), molluscs (Richardson, 1921) and oligochaetes (Brinkhurst and Chau, 1969). Furthermore, certain immature stages of insects, such as those of the Chironomidae and Simuliidae, can in fact be reared to pupation on a diet of bacteria alone (Freeden, 1960, 1964; Ivlev, 1945). Although ammocoetes were also able to utilise bacteria, the high concentration needed for growth in our experiments is probably never reached in those streams where lampreys are found (Moore and Beamish, 1973). Transforming the value for the highest bacterial concentration into cell volume gives a value of 2-3 x $10^8 \mu m^3 ml^{-1}$ a figure considerably greater than the 0.5 x $10^6 \mu m^3 \ l^{-1}$ found in the experiments employing algae. Although it is therefore surprising that lampreys were less successful when provided with bacteria this may be because, through their small size, many of the bacteria are not taken up on the mucous strands.

Although the fact that dissolved substances failed to support growth may partially reflect the relative insolubility of the fatty acid component, this should not be a totally limiting factor since the animal could presumably have mobilised some of its relatively large fat store. Since the combination of different amino acids used in this study were suitable for growth in teleosts (Mertz, 1972), it seems likely that dissolved organic substances are unimportant energy sources for natural populations of lampreys.

At 15°C, the larvae digested and absorbed an average of 39.5% of the lipid in their food, 33.8% of the protein, 35.2% of the carbohydrates and 6.5% of the cellulose (Table 31). The corresponding values for animals maintained at 5°C were 8.0%, 3.9%,

Table 31

Percentage composition by weight of the different nutritional components assimilated by larval lamprey. Values correspond to samples taken at different times during the six week experimental period.

Temperature - 15°C

Component	Percentage absorbed						Mean
Lipid	5.4	45.5	87.3	62.1	22.7	14.1	39.5
Protein	4.5	44.2	69.9	42.4	31.7	10.3	33.8
Carbohydrate	9.7	38.5	62.4	58.1	9.7	9.7	35.2
Cellulose	6.1	9.5	10.2	3.2	4.5	5.2	6.5

Temperature - 5°C

Lipid	5.5	10.5	8.0
Protein	1.5	6.3	3.9
Carbohydrate	5.1	7.3	6.2
Cellulose	0.2	0.8	0.5

6.2% and 0.5%. These data indicate that ammocoetes are inefficient utilisers of their food, a feature apparently characteristic of many organisms that feed mainly on detritus and/or algae (Ivlev, 1939; Levanidov, 1949; Brown, 1961; Wachs, 1967). It has, however, been shown that the considerable variation (0 - 35%) in assimilation efficiency in Gammarus pulex was related to variations in the length of time that the food (allochthonous leaf material) had been in the water (Nilsson, 1974). In comparison to microphagous feeders, teleosts and feeding adult lampreys normally absorb virtually all the lipid and protein they ingest (Menzell, 1960; Davies, 1963; Beamish, 1972; Farmer, 1974). Although cellulose was only utilised to a small degree, this substance is repeatedly ingested and thus broken down still further (Hynes, 1970). The inefficient utilisation of food by ammocoetes suggests that large quantities of algae must pass through the gut unharmed, a view substantiated by work on larvae on the sea lamprey where the survival rate of algal cells was approximately 45% in the summer and 90% in the winter (Moore and Beamish, 1973). This situation parallels that found in Asellus and Gammarus (page

A major problem in discussing the values for assimilation efficiency is provided by the very considerable degree of variation between the samples taken at different times during each experiment (Table 31). As suggested by Prus (1971) in his study of Asellus aquaticus where he recorded a similar situation, this could be due to one or more aspects of the experimental regime. As previously pointed out, the problems involved in his ash ratio method would have been largely overcome by the consideration of just the insoluble fraction. It seems more likely therefore that the variation in the study is due to biological factors, such as the degree of activity of the animals in the period prior to that at which the analyses were carried out. The varying pattern both of movement in the substrate (Applegate, 1950) and in the pumping of the pharyngeal chamber, which at times apparently ceases altogether (Potter, Hill and Gentleman, 1970), might in fact by themselves account for the variable assimilation efficiencies. For example, in an ammocoete undergoing movement and pronounced branchial pumping, the food might be expected to pass through the gut at a faster rate and thus be less efficiently digested and absorbed. This view is supported by the observation that in many cases at 16°C the gut takes about

54 hours to empty in an undisturbed ammocoete (Moore and Beamish, 1973), whereas within an hour it contains little food whatsoever when the animal has been removed from the substrate and left in an aquarium containing water alone. In the latter situation the animals often exhibit frequent short bursts of swimming acitivity. Similar movements by animals occupied in the experiments only a very short period of time due both to the speed of their transfer from the holding tank and to the rapid burrowing that takes place in the glass bead substrate.

In conclusion, both algae and detritus have been shown to support growth in ammocoetes, although the former is a more nutritive food source. While caution must be exercised in drawing conclusions from feeding experiments on a single species of bacterium, the data suggest that, although these organisms can be utilised, they are unlikely to be an important component of the diet of natural populations of larval lampreys. Temperature controlled the degree of utilization of algae and detritus, apparently reflecting both the decreased digestive efficiency and the greatly reduced metabloic rate under winter conditions. Although considerable variation occurred in the values for assimilation efficiency, there would appear to be little doubt that in this aspect of its biology, the ammocoete is less effective than the adults of those species which undergo a parasitic phase.

7. Lipid Deposition and Utilization in Two Closely Related Species of Lampreys, Lampetra fluviatilis (L.) and Lampetra planeri (Bloch).

Introduction

The larvae of all species of lampreys rely for food on micro-organisms and detritus filtered from the water flowing over their burrows (Creaser and Hann, 1929; Schroll, 1959; Moore and Beamish, 1973; Potter, Cannon and Moore, In press; Section 6). This stage of the life cycle, spent in the soft sediments of streams and rivers, lasts for several years and is characterized by a slow rate of growth (Hardisty and Potter, 1971a). The life cycles of the two British species of *Lampetra* differ, however, in the pattern followed by the subsequent post-larval stages. After a non-trophic metamorphosing phase of several months, the river lamprey, *Lampetra fluviatilis* (L.) migrates to sea where it feeds predominantly on teleost fishes and grows at a fast rate(Hardisty and Potter, 1971b). This species ceases feeding as it re-enters fresh water on its way upstream to the spawning grounds, a migration that takes several months. The life cycle of the derivative brook lamprey, *Lampetra planeri* (Bloch), contains no adult parasitic stage, the whole of the seven to nine month post-larval phase being restricted to fresh water (Hardisty and Potter, 1971b,c). Since this phase culminates in spawning, the periods of metamorphosis and gonadal development in this species occur concomitantly.

Clearly, by the end of their larval and adult feeding stages, anadromous lampreys must have laid down sufficiently large lipid reserves to act as an energy source throughout the whole of the subsequent lengthy non-trophic periods of metamorphosis and the upstream spawning migration. Furthermore, the patterns of lipid deposition and utilization in parasitic lampreys provide an interesting comparison with those taking place during the divergent life cycle of its closely related and derivative non-parasitic species. During the larval phase, a marked seasonal variation in lipid content has been found both in the brook lamprey *L. planeri* (Hardisty, 1961) and in the sea lamprey, *Petromyzon marinus* L. (Lowe, Beamish and Potter, 1973), with maximum values occurring in the late spring and early summer. The latter of these studies also demonstrated that a great increase in lipid deposition occurred in the period prior to transformation, at which time the animals show little or no increase in length. Following this " arrested growth phase " (see Hardisty and Potter, 1971b), the levels then decline precipitously during metamorphosis. With respect to the adult stages, data on the upstream migrating river lamprey show that lipid levels decrease from values corresponding to about 45% of the dry weight in the autumn to as low as 14 - 15% at spawning in the following spring (Hardisty, 1956; Bentley and Follet, 1965). In the brook lamprey, the data of Dines (1973) indicate that the amount of lipid retained through the metamorphosing period may in some cases be as low as 20% of the original value.

The methods of lipid extraction and the means by which the data have been expressed have, however, varied considerably in studies on lampreys and this has to some extent hindered comparisons between life cycle stages and between different species. Furthermore, there are several aspects of lipid deposition and utilization in closely related parasitic and nonparasitic " paired species " (Zanandrea, 1959) that have not as yet been investigated. This study has therefore determined lipid levels throughout the life cycle of L. planeri and during the metamorphosis and upstream migration of L. fluviatilis. Particular attention has been paid to the biological significance of the differing lipid levels in terms of feeding status, migratory movements and the degree of gonadal development. The relative amounts of neutral and phospholipids have also been ascertained and preliminary data are provided on their fatty acid composition.

Materials and Methods

Electrofishing was employed to collect larval and post-larval representatives of L. planeri from Highland Water and the metamorphosing stages of L. fluviatilis from the Teme, a tributary of the Severn, and from the River Towy (Breconshire). Samples of larval L. planeri were also collected in May from the River Chew (Somerset). Adult river lampreys were taken from the intake screens of the Oldbury Power Station in the Severn Estuary, from the dam at Tewkesbury on the River Severn at a time soon after the animals had entered fresh water and later from their spawning grounds in the River Teme.

For studies on larval feeding, the animals were immediately after capture placed in the fixative described by Steedman (1974). Later, in the laboratory, material was removed from the ammocoete gut by making a longitudinal cut in the intestine and scraping the contents on to a microscope slide. The material was mounted in distilled water and examined at a magnification of 400 times, the identification and counting of the algae then being carried out in the manner described by Moore and Beamish (1973). The dry weight of the gut contents was ascertained after drying by sublimation for 12 h, after which time constant weight had been reached. The total number of cells in the gut was estimated after oxidization of the gut contents of each animal in a know amount of concentrated HNO_3 and counting the number of cells in three 0.1 ml aliquots. These data were converted into cell volumes as outlined on page 6. Measurements of the length and diameter of the compacted food in the gut then enabled an approximate estimate to be made of the total volume of food. From the above data on volumes of algae and the total volume of food present in the animals, it was possible to gain some idea of the contribution algae make to the diet of ammocoetes.

After transportation to the laboratory, the animals to be used for lipid analyses were placed in a deep freeze for fifteen minutes and then weighed to the nearest 10 mg. In the case of ammocoetes, the whole animal was dried by sublimation, homogenised, and the total lipid extracted in chloroform/methanol (Folch, Lees and Stanley, 1957). The phospholipid fraction was determined by ashing duplicate 1.5 mg lipid aliquots with sulphuric and perchloric acids (3:2, vol vol), estimating the total weight of phosphorus and multiplying this value by 25 (Chen, Toribara and Warner, 1956). The fatty acid composition of the separate neutral and phospholipid fractions was determined by the method described by Hunter and Rose (1972), except that the flow rate was increased to 90 ml min^{-1} to facilitate analysis of the C_{20} and C_{22} acids. Ashing was also carried out at 550°C for 24 h on separate whole larvae.

Lipid determinations were also made in the same manner on metamorphosing L. planeri , apart from the more mature individuals in which the gonad was removed. Separate measurements of the two components in the latter cases enabled the amount of lipid in the whole animal, as well as in either its ovary or testis, to be calculated. The same procedure was also adopted for the very much larger upstream migrants of L. fluviatilis, except that in this stage the liver was also taken out and used for separate analysis. In both metamorphosing L. planeri and adult L. fluviatilis, determinations were also made of the relative neutral and phospholipid fractions and of their fatty acid composition.

For a study of metamorphosis in L. fluviatilis, 70 individuals caught at the commencement of transformation and with lengths ranging from 8.4 - 11.1 cm , were kept in the laboratory in tanks containing a soft natural substrate into which they would readily burrow. The photoperiod and temperature were changed throughout the ensuing months to parallel conditions in the River Severn. Subsamples of ten animals, taken at intervals for estimates of wet weight, lipid and moisture content, provided data both on changes in the relative levels of these components as well as providing an approximation of what was taking place in terms of actual values.

Results

A comparison between the composition of the species of algae in the gut of larval lampreys from Highland Water and that found floating in the water (potamoplankton) and lying on the sediment (epipelic assemblage), showed that all the main non-filamentous algae in the environment were ingested by L. planeri (Table 32). Furthermore, in several cases, a rise in the numbers in the environment was accompanied by an increase in their relative abundance in the gut, examples of this being provided by Nitzschia dissipata in November, by Pinnularia biceps and Synedra rumpens in May, and by Achnanthes minutissima in August. No consistent pattern of selection was exhibited by larval lampreys for the microflora of either the potamoplankton or the epipelic assemblage, a finding paralleling that for similar algal genera in species of lampreys from Canada and Australia (Moore and Beamish, 1973; Potter, Cannon and Moore, In press).

Data interpolated for a 1 g ammocoete from linear logarithmic equations relating the number of cells in the gut to the weight of the animal, demonstrate a marked seasonal variation in the volume of algae ingested (Fig. 70b). Minimum levels (0.1×10^6 μm^3) were found in November, after which there was a slow rate of increase through to March, the volumes then rising markedly with peak values ($8 - 9 \times 10^6$ μm^3) being attained in May and July. This period was followed by a rapid decline through to the samples taken in early November. In terms of numbers, the values followed a similar seasonal pattern but with peaks occurring later, namely in the period between July and September (Fig. 70b).

During the winter months in Highland Water, the algae contributed between 0.01 and 0.02% towards the total volume of the gut contents, this value rising, however, to between 0.1 and 0.3% in the summer. In the River Chew, on the other hand, the values in May were as high as 1.5%. These results compare with peak percentage volumes of 0.9% in sea lampreys taken from a Lake Ontario tributary (Moore and Beamish, 1973). It is important to remember, however, that all these estimates are undoubtedly of a conservative nature, as they also were in the similar study of feeding in Asellus and Gammarus (Section 5).

Table 32. Species composition (%) in Highland water of some important non-filamentous algae sampled from the sediment (S), the potamoplankton (P) and the gut (G) of larval lampreys.

	MAY			AUGUST			NOVEMBER			FEBRUARY		
	S	P	G	S	P	G	S	P	G	S	P	G
Achnanthes minutissima v. *cryptocephala*	5.5	13.0	10.0	6.5	28.0	22.5	10.5	3.5	25.0	7.0	3.5	8.0
Achnanthes saxonica	3.5	10.5	4.5	27.0	12.5	12.0	5.0	22.5	18.5	8.0	21.0	10.0
Cymbella naviculiformis	7.5	0.5	15.0	20.0	0.5	2.0	5.0	0.5	9.0	8.0	0.5	9.5
Eunotia exigua	0.0	0.5	0.0	0.5	0.0	0.0	6.0	0.5	2.0	3.0	3.0	1.5
Navicula spp.	6.0	7.0	4.5	3.5	3.0	5.5	7.5	2.0	2.0	2.5	12.0	15.5
Nitzschia dissipata and varieties	2.5	1.0	1.0	7.0	1.0	9.0	1.0	20.5	14.5	1.0	5.5	1.0
Pinnularia biceps	58.0	0.5	35.0	0.5	0.5	3.0	5.0	0.1	10.0	25.5	0.5	11.5
Pinnularia viridis	6.5	0.0	0.5	3.0	0.0	0.0	4.0	0.1	0.2	10.5	0.1	1.0
Synedra rumpens	3.0	24.0	7.5	0.5	0.5	0.0	0.5	0.0	0.0	0.0	0.1	0.0
Synedra ulna and varieties	4.5	21.5	7.5	6.0	1.0	4.5	2.5	4.0	1.0	5.0	0.5	0.5
Chlamydomonas spp.	1.5	0.5	0.5	21.5	27.5	20.5	0.0	0.1	0.1	0.0	10.5	7.5

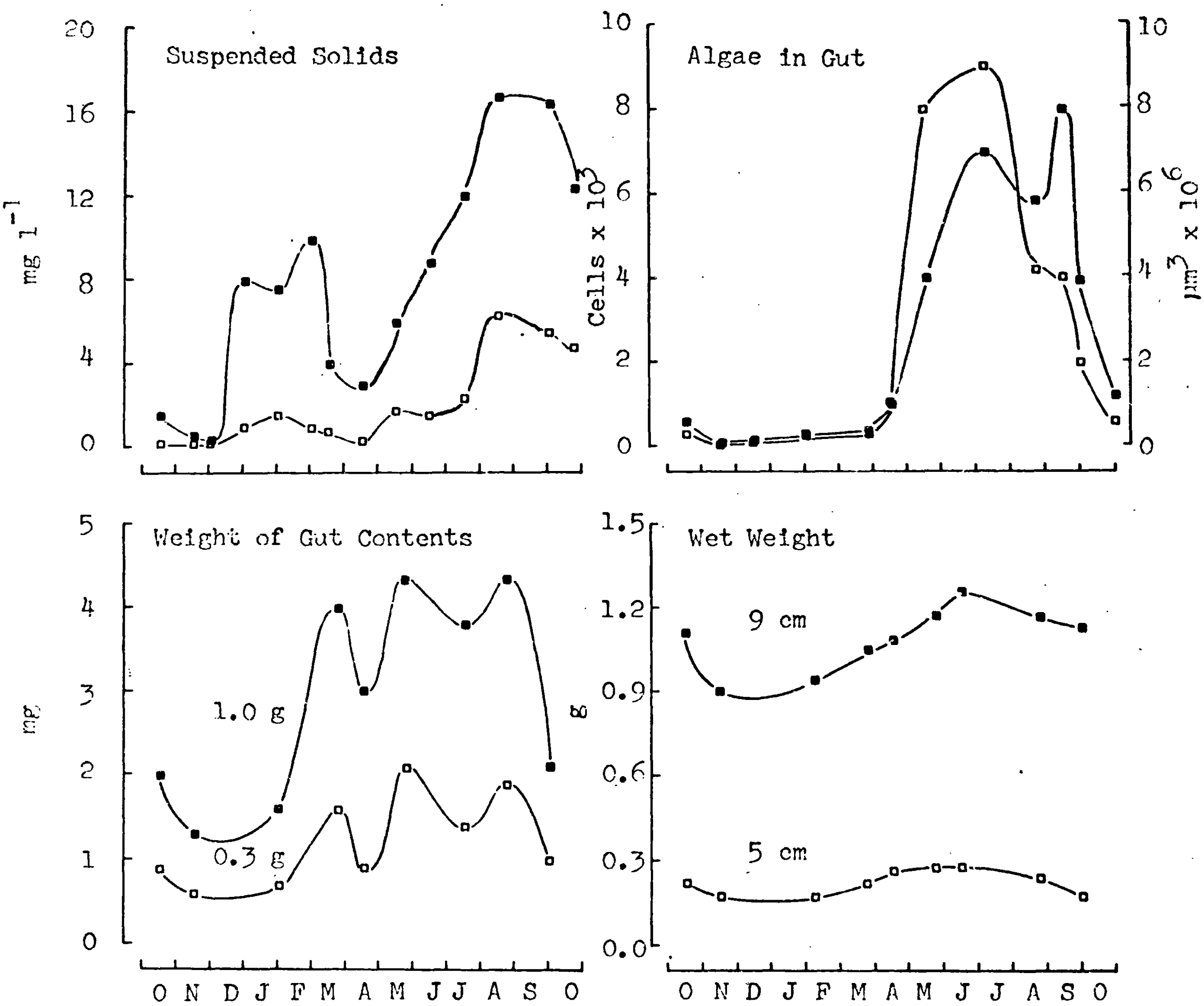

Fig. 70a. The dry weight of suspended solids (■) and their organic fraction (□) in Highland Water after filtration of samples through a 1.2 µm Millipore membrane.

b. The volume (□) and numbers (■) of algae in the gut of larval L. planeri at different times of the year. Each point represents the calculated value for an ammocoete whose wet weight is 1 g.

c. The weight of gut contents of larval L. planeri at different times of the year. Values have been calculated for ammocoetes with a wet weight of both 0.3 and 1.0 g.

d. The wet weight of larval L. planeri at different times of the year. Values have been calculated for ammocoetes with a total length of both 5 and 9 cm.

Since algae formed a relatively small component of the diet, the detritus fraction of the suspended solids must almost certainly be of importance as a food source. In Highland Water, the suspended solids, most of which would have consisted of non-living material, showed a small peak in January and February , clearly associated with the effects of scouring caused by the heavy flooding that occurred at that time, and another larger peak in the early autumn, presumably due to the discharge of decaying plant material into the water (Fig. 70a). A reduction in the amount of suspended solids in the environment in April was paralleled by a decline in the weight of the gut contents at this time (Fig. 70c). However, the retention of similar peak values for the amount of material in the gut in March, June, August and September, differing from the pattern of variation seen in the suspended solids in the water, suggest that in general the level of detritus was rarely a factor limiting the amount the animal could ingest.

The wet weight of ammocoetes, as with the weight of gut contents interpolated from linear logarithmic equations, showed a gradual seasonal change with peak values being attained in the summer (Fig. 70d).

At the sampling site in Highland Water, L. planeri was almost always found to metamorphose at total length greater than 11 cm. Since this species exhibits little or no increase in length after it has reached transforming size (Hardisty and Potter, 1971a), each sample of larvae which always contained at least 20 animals, was separated into individuals whose lengths were greater and less than this value. For ammocoetes in the smaller length category, a calculation was then made of the linear logarithmic relationship between each of moisture, lipid and ash, and the wet weight of the animal. The regression slopes varied in the case of moisture between 0.9357 and 0.9774, for lipid between 1.1369 and 1.3109, and for ash between 0.9583 and 1.1121. From the above regression equations, the percentage amount of moisture, lipid and ash was then calculated for ammocoetes of 0.3 and 1.0 g representing animals near the extremes of weight always found in this size category. In the case of the larger ammocoetes, which lay within a narrow length range of 11 to 13 cm, the values in the following account are based on means.

All ammocoetes showed a marked seasonal variation in both moisture and lipid (Fig. 71). Peak values of the latter occurred in May

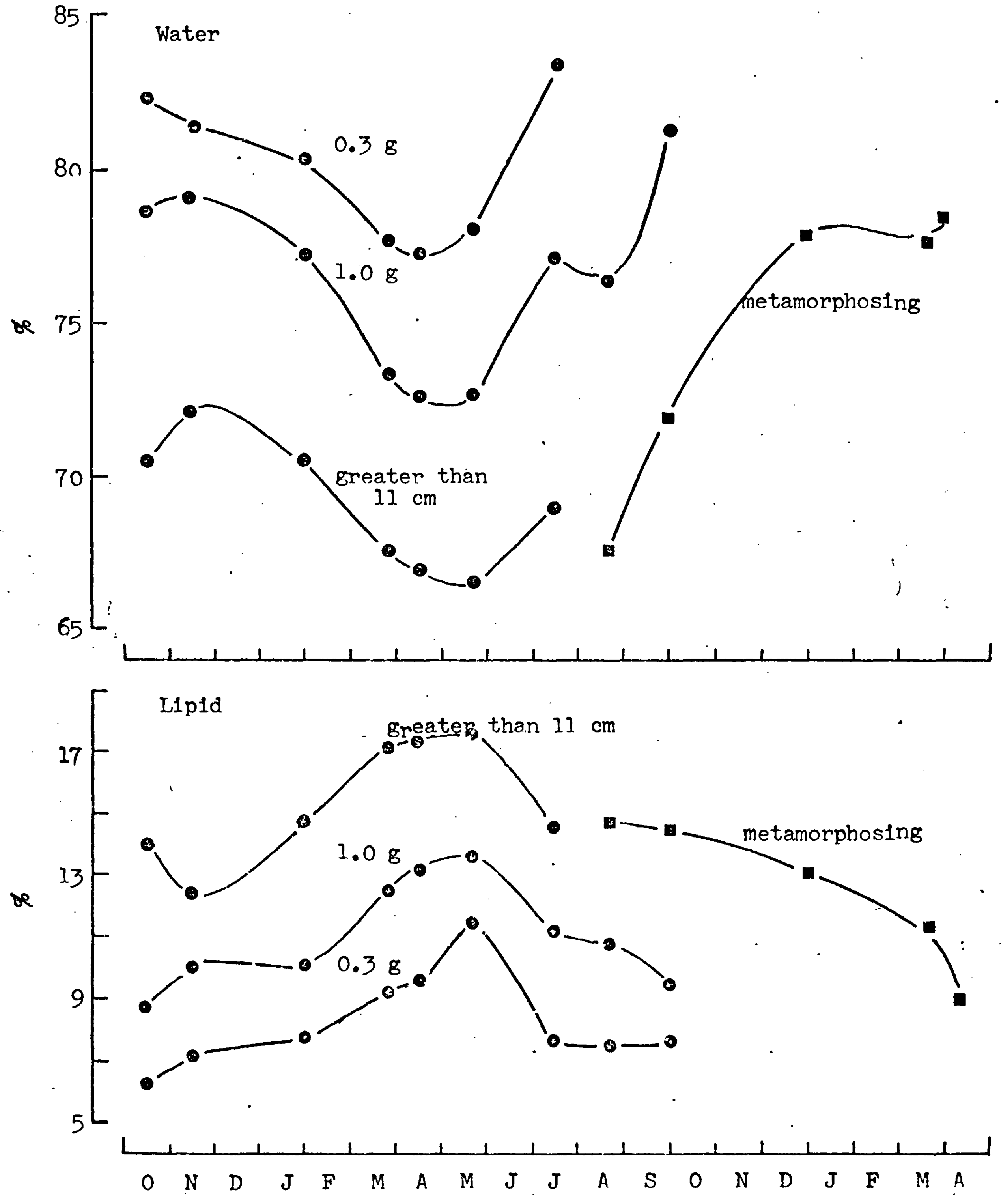

Fig. 71. The moisture and lipid content (as % wet weight) of larval and metamorphosing L. planeri. For ammocoetes less than 11 cm, values are calculated on the basis of wet weight of 0.3 and 1.0 g, while those for both ammocoetes greater than 11 cm and the metamorphosing stages represent means.

while the lowest were recorded in October and November, a pattern converse to that found with moisture. The data also clearly show that there is an elevation in lipid content as the ammocoetes become older with larvae greater than 11 cm attaining peak levels of 17.5% compared with 11.5% in an 0.3 g animal measured at the same time. Furthermore, the relative amount of phospholipid was always greater in the smaller individuals (Table 33), although the difference was generally not significant. The amount of ash remained at between 0.95 and 0.99 throughout the period between March and August before declining to values of about 0.90% through the winter months.

During metamorphosis, lipid values declined and the moisture content rose. The terminal values for L. planeri represented animals that were still burrowed and although they had developed secondary sexual characters the eggs were still bound in the mesovarium. Unfortunately, frequent attempts to capture spawning individuals were unsuccessful, a feature almost certainly attributable to the fact that, because of the cold spring in 1975, the spawning season was delayed and ultimately completed within a very short space of time.

In the river lampreys held in the laboratory from the beginning of transformation, the percentage amount of lipid declined throughout the metamorphosing period from the initial levels of 14.1% to terminal levels of 7.9% (Fig. 72). The rate of loss was, however, more pronounced near the beginning of transformation than at the end. Likewise, the relative gain in moisture was greater over the early stages and showed a marked slowing down near the end (Fig. 72). The overall change in moisture was from 71% in September to 80% in the middle of March. Since the mean percentage for eight animals caught in the River Towy towards the end of February (8.9%) was similar to that recorded in the laboratory during this month, it seems likely that the changes recorded in the laboratory parallel those occurring in the field.

While the actual amount of lipid also declined more precipitously at the beginning than at the end of metamorphosis, the actual amount of moisture showed a rise initially and then a precipitous decline between the beginning of November and early December (Fig. 72). This decline, together with small loss of lipid at this time, result

Table 33. The relative amount of phospholipid in the total lipid fraction of lampreys at various times and at different stages of development. Sample size in each case is 5.

Species	Stage		Time of sampling and relative amount of phospholipid (mean % ± I.S.E.)			
			December	April	August	October
	Ammocoetes	11 cm	21.2 ± 1.50	9.5 ± 0.31	12.6 ± 0.77	14.1 ± 0.34
<u>Lampetra</u>	Ammocoetes	11 cm	19.1 ± 0.92	8.9 ± 0.75	9.5 ± 0.25	-
<u>planeri</u>			October	December	January	March
	Post-larval stages		10.7 ± 0.61	16.6 ± 1.34	21.7 ± 1.60	40.2 ± 1.31
			10.5 ± 0.96	15.8 ± 1.14	21.5 ± 2.04	41.1 ± 1.40
			October (early upstream migrants)	April (spent animals)		
<u>Lampetra</u>	Adults		20.2 ± 0.45	77.8 ± 2.29		
<u>fluviatilis</u>			19.7 ± 0.50	85.5 ± 6.17		

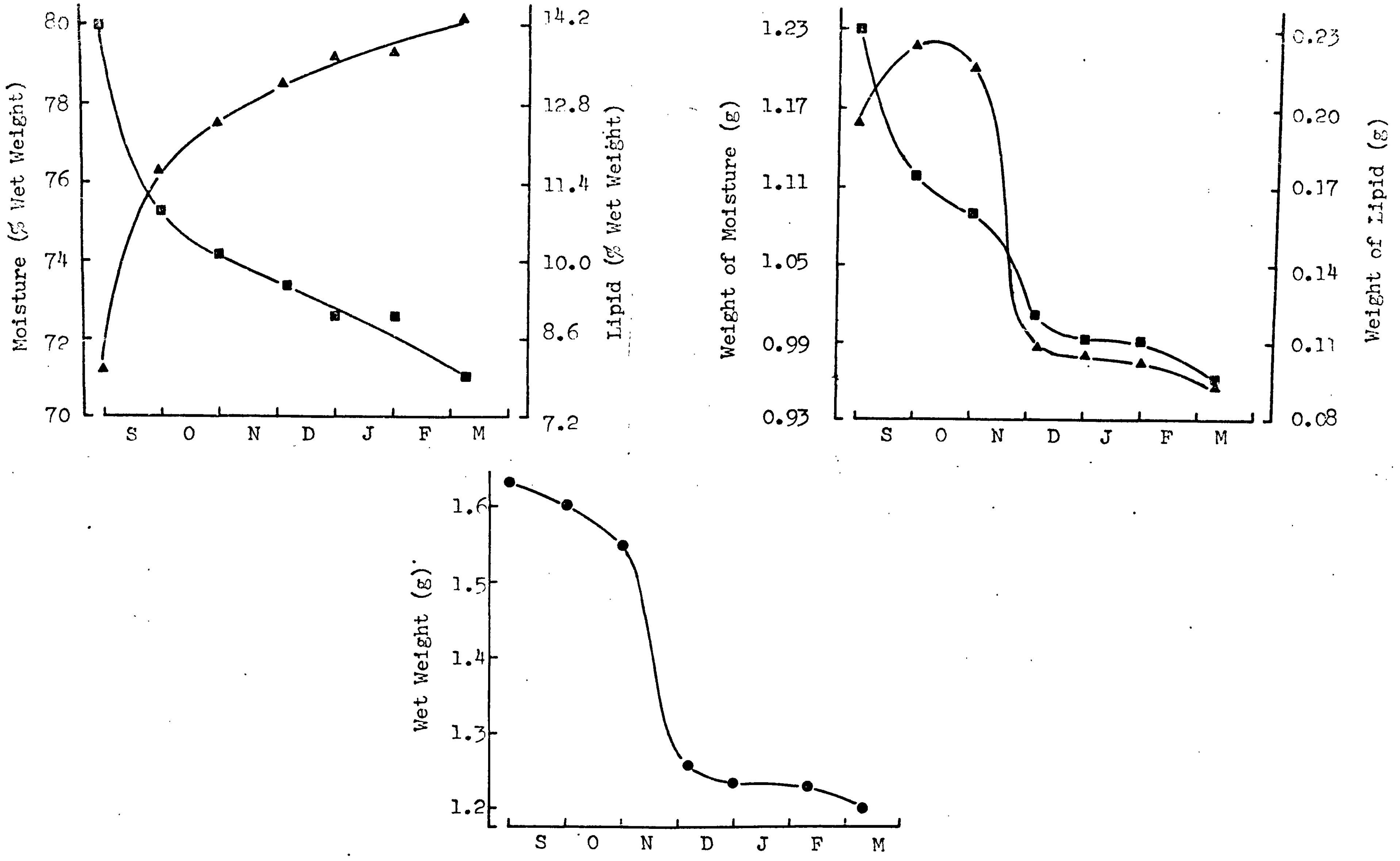

Fig. 72. The amount of moisture (▲) and lipid (■) in _L. fluviatilis_ held in the laboratory throughout metamorphosis expressed both as a percentage and as actual values. The third graph shows changes in wet weight.

in a very marked reduction in the wet weight of the animal at this point in metamorphosis. The rate of loss in both water and wet weight is relatively slow between December and the middle of March. In actual terms, therefore, water can only increase to accomodate a loss in lipid for a limited amount of time. The percentage decline in wet weight over the whole of the metamorphosing period from September 1 to the middle of March was 26%.

The size of the gut and the occasional presence of food in the intestine of adult river lampreys caught between October and early December in the Severn Estuary at Oldbury, clearly demonstrated that these animals were either still feeding or more usually had just completed the adult trophic phase. On the other hand, the adults of this species taken at a similar time in fresh water at Tewkesbury had clearly finished feeding for some while. Although the total lipid levels of males and females in the autumn did not differ significantly ($p > 0.05$) at either Oldbury or Tewkesbury, the values obtained from the latter of these two sites did show a significant decline ($p < 0.01$) from those obtained in the estuarine environment. The same situation also pertained with respect to the lipid contained in the body after removal of the gonads and liver, a component subsequently referred to as muscle. In the autumn, the relative levels of lipid in the liver of males did, however, differ significantly ($p < 0.001$) from those of the females at both Oldbury and at Tewkesbury but no significant difference ($p > 0.05$) was found between the samples of either the males or the females from these two locations at this time. In both sexes, both the total amount of lipid and the levels of lipid found in the muscle declined throughout the spawning run, the rate of loss being particularly marked in the period around spawning. Although the amount of lipid in January was, as before, significantly lower in females than in males, the relative amount in both sexes had been depleted to almost exactly the same level by the completion of spawning.

The absence of a difference in the amount of lipid in male and female adult L. fluviatilis is in agreement with the findings of Bentley and Follett (1965) based on animals held in the laboratory until they had reached sexual maturity. The difference in liver lipid levels between the sexes also parallels the similar differences found in this study at various stages in the spawning run but not, it should be remembered, after spawning has just been completed. Like Bentley and Follett, a significant difference ($p < 0.05$) was found between the relative amount stored in the musculature of animals prior to spawning but it should be noted that no such difference was found at any other stage of the spawning run (Fig. 73).

With respect to the gonads there is a small decline in the percentage lipid in the ovary and a more pronounced loss in the testis. In both cases, however, it should be remembered that whereas the whole animal and most of its organs are undergoing a marked reduction in weight during the upstream migration, very much the opposite pattern is taking place in the gonads. Thus, although in relative terms the latter are losing lipids, the ovary in particular is actually gaining very considerably in the total amount of lipid it contains. This point is well illustrated by the fact that the mean weight of lipid in the ovary of the early migrants caught at Oldbury in the autumn was 0.86g whereas at sexual maturity it was 1.94 g. On the other hand, the total amount of lipid in the whole animal averaged 9.25 g in males and 9.54 g in females at the commencement of the migration, declining to 2.5 and 4.7 g at maturity and 1.36 and 1.14 g after spawning. While caution has to be exercised in drawing conclusions from these data based on actual values taken from animals caught at different times and different sites during their migration, the fact that the animals appeared to represent a reasonably homogeneous population and were caught in the same river system, suggests that they give a fair idea of the change that takes place in actual levels. While the massive decline in total lipid in the females between maturity and the cessation of spawning can clearly be largely attributed to the loss of eggs, the decline in males is probably at least in the main due to lipid utilization. Such a view is consistent with the observation that at this time there is a marked rise in the standard and active rates of oxygen consumption (Claridge and Potter, In press). In this context, it is also worth noting that Larsen (1973) has pointed out that lowering the temperature and removal of either the hypophysis or the gonad prolongs survival through slowing down mobilization of body tissue.

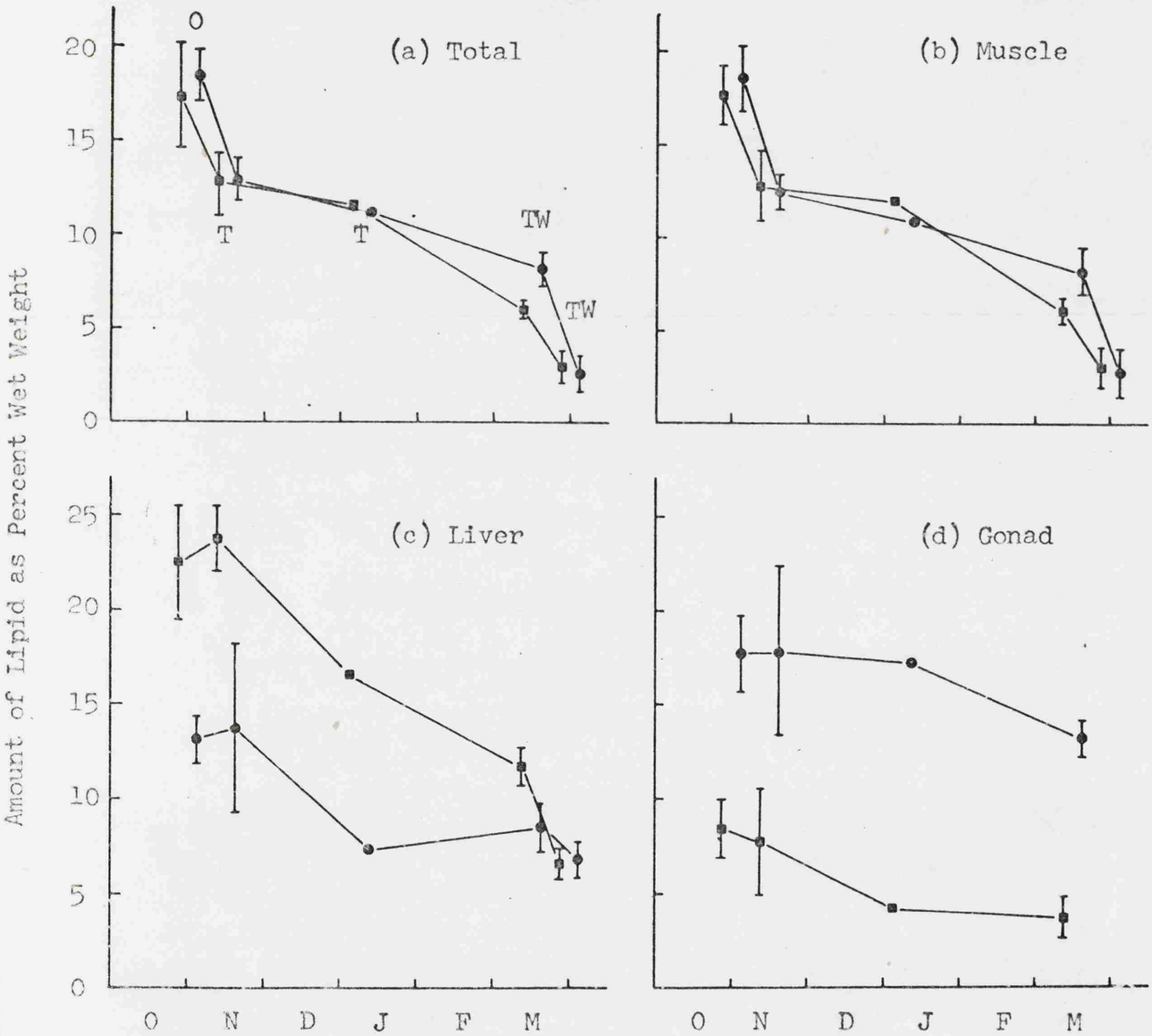

Fig. 73. The amount of lipid found in male (■) and female (●) adult L.fluviatilis and the amount recorded for its musculature, liver and gonad. Each value is expressed as a percentage (mean ± 95% confidence limits) of the animal's wet weight. Apart from the January collection which consisted of four males and four females, the samples always contained between 6 and 14 individuals of each sex. The collection sites are indicated by the symbols "O" (Oldbury), "T" (Tewkesbury) and "TW" (Tenbury Wells).

Another useful way of comparing lipid levels in the organs and between different stages in the life of the spawning run is to consider this component in terms of the amount found in each structure as a percentage of the total amount present in the whole animal. Thus, while over 90% of the lipid is deposited in parts of the body other than the gonads and liver in both the early migrants and the mature males, the position is entirely different in the mature females where over 40% is located in the gonads.

A progressive decline in the amount of neutral lipids occurs between the commencement of the upstream migration, where it forms about 80% of the total lipid, and that found at spawning when it comprises only 14 - 21% (Table 33). The high level of phospholipids at the termination of the life cycle bears out the suggestion of Bentley and Follett (1965) that the lipids remaining at this time probably represent "structural materials".

The predominant fatty acids in the neutral lipids of ammocoetes shorter than 11.0 cm occurred in roughly similar amounts during both the period of maximum lipid deposition (June) and in the winter, with 16:1 and 18:1 being most common, followed in order of descending importance by 16:0, 14:0 and 22:6 (Table 34). The predominant fatty acids in the phospholipids, on the other hand, were 18:1, 18:2, 16:0 and 16:1, all of which occurred in approximately the same amount, followed by 22:6 and 14:0. Since the proportion of these latter fatty acids was similar throughout the year, as was also the case with the neutral lipids, ammocoetes of L. planeri apparently fail to exhibit selective utilization of fatty acids during the year, a feature previously reported for some teleosts such as the cod Gadus morhua (Jangaard, Ackman and Sipos, 1967).

Despite the fact that L. planeri undergoes considerable morphological change during the early stages of metamorphosis, transforming specimens captured in October exhibited virtually the same fatty acid spectrum as that of the ammocoetes (Table 34). However, later in the life cycle, the relative amounts of several unsaturated lipids decreased. This feature has been noted in starving teleosts and presumably indicates selective utilization of the unsaturated fatty acids (Lovern, 1938). The only difference between Lovern's (1937) work on the fatty

Table 34. Relative abundance (%) of the various fatty acids in neutral and phospholipid fractions of *Lampetra planeri*.

	Ammocoetes (June)		Metamorphosing (January)	
	Neutral lipids	Phospholipids	Neutral lipids	Phospholipids
14 : 0	6.5	6.5	10.8	8.7
15 : 0	4.7	2.0	6.5	1.3
16 : 0	16.9	15.8	12.0	16.0
16 : 1	27.2	17.3	26.0	15.3
16 : 2	4.1	3.0	3.0	2.0
18 : 0	2.9	5.0	3.1	1.5
18 : 1	24.0	18.5	23.5	17.3
18 : 2	1.3	12.1	1.1	17.1
18 : 3	0.8	4.5	0.5	0.5
20 : 5	4.5	6.5	3.5	6.8
22 : 5	0.1	0.5	Trace	0.8
22 : 6	7.0	8.3	10.1	12.7

acids of what were presumably adult lampreys and the ammocoetes in this study were the higher levels of unsaturated C_{20} acids in the former investigation.

Discussion

It has been customary to attribute the increase in lipid content in the spring and early summer to the bloom in algae that occurs at this time (Hardisty, 1961; Lowe et al., 1973). Although maximum lipid deposition in Highland Water was also approximately coincident with the peak in the volume of algal cells both in the potamoplankton and the epipelic assemblage (Figs 13,18), it would for two main reasons appear necessary to look also for other additional factors. For example, the actual algal component of the gut was always relatively low (0.01 - 0.3%), a feature reflecting the paucity of the flora in the New Forest stream (page 23). A second factor of some importance is that the standing crop of both the potamplankton and the epipelic assemblage remained at similar low levels during March and April at a time when the lipid levels were beginning to show a sharp rise. Since, however, temperature was beginning to increase during these latter two months it may have been exerting an influence on various aspects of the animals physiology. Temperature is known for example to influence not only the metabolic rate (Hill and Potter, 1970) but also the digestive efficiency and the rate at which the food passes through the intestine (Moore and Beamish, 1973; Section 6). The rise in lipid deposition may therefore be due to a greater utilization of any food present in the environment in the spring than during November, December and January. Further support for such a view is provided in this study by the fact that the volume of algae in the gut started to rise between March and April whereas no such elevation could be detected in the volume of the algal population in the environment (Figs 13,18). Of even greater importance, however, is the very great increase in the total weight of the gut contents in March, with these much higher levels generally being maintained through the ensuing months until August.

It is also of interest that although lipid levels declined in July and August, the actual amount of material in the gut remained at a relatively high level. While the reduction in the volume of algal cells in both the water and on the sediment at this time may partially contribute to this phenomenon, it seems equally likely that the reduction may represent a switch from lipid storage to protein anabolism and growth.

The above discussion should not give the impression that algae, although small in relative terms in the gut, are not considered an important component of the diet. For example, from laboratory studies it is clear that growth occurs far more rapidly when ammocoetes are fed algae than when they are provided with detritus (Section 6). Furthermore, there was also evidence that the much higher condition factor in ammocoetes taken from the River Chew than those from Highland Water was correlated with a higher algal component in the gut, a feature related to the much greater productivity of the former of these environments. This feature may also be related to the much larger size attained at metamorphosis by brook lampreys from the Chew.

The marked seasonal variation in the relative amount of lipid in larval L. planeri, with peak values occurring in May, parallels the data of Hardisty (1956; 1961) for a population from a more productive stream. While the seasonal pattern is also similar to that found in a larval population of P. marinus in a Lake Ontario tributary (Lowe et al., 1973), in contrast to L. planeri the percentage amount of lipid in the sea lamprey does not rise significantly during the period prior to the attainment of transforming size. Thus, whereas values for a brook lamprey in July/August are as high as 11.8%, the level in the sea lamprey is only about 6% at this time. Since both species enter metamorphosis, however, at a time when they contain much more comparable mean levels, i.e. 13.5 and 14.6% respectively, it follows that the "arrested growth phase" in the sea lamprey is one in which a relatively far greater amount of lipid has to be deposited to reach those found at the commencement of transformation. This feature may in fact provide an explanation as to why in the late summer there are always a relatively much larger ratio of transforming brook lampreys to large ammocoetes in populations of this species than is the case in comparable samples of the sea lamprey (cf. Hardisty, 1961, 1969; Lowe et al., 1973; Beamish and Potter, In press). In other words, since the time required to achieve "threshold" lipid levels for metamorphosis in P. marinus is probably much greater, the "arrested growth phase" must almost certainly last for a longer period in this species, a view also suggested on the basis of an analysis of length-frequency data for a population of anadromous sea lampreys in New Brunswick (Beamish and Potter, In press).

In the general context of metamorphosis and lipid levels, it is noteworthy that Dines (1973) found the relative lipid levels of transforming brook lampreys were virtually identical in the three entirely different river systems he investigated. Since these rivers varied greatly in terms of the abundance of their microflora, it would appear that the threshold lipid levels for metamorphosis are independent of environmental conditions and that each species may have a characteristic value.

In L. fluviatilis from the River Severn system , the lipid levels at the commencement of metamorphosis (c. 14%) are lower than they are at the commencement of the upstream migration (c. 18%). This is despite the fact that the duration of the initial non-trophic period tends to be longer in river lampreys than is generally the case with the upstream migrating individuals (Hardisty and Potter, 1971b; Potter and Huggins, 1973). This feature is probably correlated with the fact that, in the adult river lamprey, sufficient food stores have to be laid down during the marine trophic phase to facilitate both the upstream migration and the maturation of the gonads. By contrast, although considerable morphological and physiological changes do take place during metamorphosis, individuals at this stage of development spend most of their time burrowed until they are ready to embark on their downstream migration. Since this migration is also of a more passive nature than that of the adult and as little development of the gonads occurs during metamorphosis (Hardisty, Potter and Sturge, 1970), the metabolic requirements of the animal are clearly less than that of the adult. This view is supported by the fact that lipid levels are still as high as 8 - 9% at the time when the animal is passing from fresh water to a marine environment compared with terminal values of about three percent in the spawning adult.

The lipid levels for L. planeri at the commencement of metamorphosis (14.6%) are similar to that of early transforming L. fluviatilis but lower than the values recorded for adult river lampreys at the begining of the spawning migration. In contrast, however, to the upstream migrants, the post-larval stages of the brook lamprey remain burrowed until just prior to spawning when they undergo only a short upstream migration to the spawning grounds (Hardisty and Potter, 1971a).

While there is enormous development of the gonads during the post-larval period, it is possible that since the level of oocyte atresia is exceptionally high, there may be a considerable amount of recycling of ovarian material (Hughes and Potter, 1969). Thus, as with the metamorphosing _L. fluviatilis_, the total metabolic demands placed on the metamorphosing and adult brook lampreys are probably much less than on upstream migrating river lampreys.

8. Some Aspects of the Biology of Crustaceans in the Severn Estuary

Introduction

Although crustaceans occur abundantly throughout most estuaries in the British Isles (Milne and Dunnet, 1972), there is only a small amount of literature on many aspects of their biology relevant to studies on the feeding of fishes. There appears, for example, to be data of only a more general nature for several species of amphipods and calanoids (Sexton , 1942; Spooner, 1947, 1951), while detailed studies on mysids are largely restricted to Scottish populations (Mauchline, 1967 - 1971). Similarly, comprehensive investigations concerning isopods are limited to the work of Fish (1970) and Jones (1970a,b). A considerable amount is known, however, about decapods, particularly through the work of Lloyd and Yonge (1947) and Meredith (1952) on Crangon crangon (L.) (Crangon vulgaris Fabricius). The primary purpose of this investigation was therefore to describe some aspects of the reproductive biology, vertical distribution, growth and abundance of the predominant crustaceans in the Oldbury region of the Severn Estuary. In several cases, these data could be compared with the initial surveys of Bassindale (1941, 1942) and the detailed investigations of Lloyd and Yonge (1947) carried out prior to changes in thermal and other factors in this region through the introduction of Power Stations.

Material and Methods

Day-time sampling was carried out at a minimum of two weekly intervals from the Oldbury-on-Severn Nuclear Power Station (Lat. 51° 39' ; Long. 2° 34') between the middle of December 1973 and the middle of April 1975. The samples, collected from the cooling intake, were always taken in the 1 - 2 h before high tide. Since the intake at this station was drawn from a reservoir through a series of vertical bars approximately 23 cm apart, larger objects are excluded from entering the pits at the commencement of the cooling system. Water is drawn from the pits through a large vertical wheel containing a grill with a mesh of 1 - 2 cm. While most of the water passes through to the main part of the station to cool the reactors, a small amount of water is diverted along a sluice. This latter flow is used to convey organisms and debris extracted by the wheel's mesh work into collection bins. By placing a plankton net (mesh size, 0.5 mm; diameter at the mouth, 28 cm) over the open end of the sluice, collections could be made of the organisms passing through.

The inlet for the Power Station, measuring approximately 1.3 m in height, was situated immediately adjacent to the floor of the reservoir. This meant that, at low tide, the entire water column was drawn into the station while, at high tide, only the lower portion was extracted. During periods of low water, objects on the surface of the reservoir could be seen to be drawn into the station from a distance of 30 m or more at a rate of at least 10 cm sec^{-1}.

The major advantage in sampling from the intake current was that collections could be made with a minimum of equipment under any weather or tidal condition. Since small organisms easily pass through the mesh work on the wheel, their abundance in the sluice probably approximates to that found in the environment. However, in the case of larger organisms the screening process has concentrated their numbers so that the density of these animals in the sluice would be considerably higher than would be found in the environment.

Samples of crustaceans were also collected in several instances from vertical and horizontal hauls made in the reservoir using the plankton net whose dimensions were given above. Approximately 15 m^3 of water were filtered during each collection. In addition, to these samples, benthos was occasionally collected throughout the reservoir using a 21 x 15 x 15 cm grab and from outside this area by hand.

The reservoir, which provided a continuous flow of water to the intake, had an area about 2 km^2 with an average depth of 0.5 - 1.2 m at low tide. It was built out over the intertidal flats and was flooded for at least eight hours each day during the periods of high water. Bottom deposits consisted mainly of organically rich sand and few if any macrophytes. Maintenance crews from the Power Station periodically dredged about 5% of the bottom of the reservoir and deposited the sediments nearby. The heated effluent produced a blum of water 5 - 12 $^{\circ}$C warmer than ambient conditions skirting the outside of the reservoir. The turbidity of the estuary varied a great deal but usually remained relatively high, i.e. greater than 50 JTU. In many areas outside the reservoir, bottom deposits were relatively hard with both rocks, measuring up to 50 cm in diameter, and macrophytes occurring in large quantities.

In the laboratory, the animals were sexed and measured from the tip of the rostrum to the insertion of the telson, except in the case of Crangon crangon, where, for comparability with other workers (Lloyd and Yonge, 1947), the lengths were taken from the tip of the rostrum to the tip of the telson. The reproductive state of the organisms was also noted.

The algal content of the reservoir water was determined at monthly intervals by filtering one litre of water through a Sartorius membrane (pore size: 0.45 μm) and examining the filtrate at a magnification of 400 times. The amount of suspended solids in the reservoir was determined from 400 - 500 ml samples of water using the method described on page 64. Water temperatures were taken at mid-day throughout the study and occasional determinations were also made of salinity.

Results and Discussion

Environmental Conditions in the Reservoir

Water temperatures recorded near high tide increased from about $7^{\circ}C$ during the winter of 1973 - 1974 to 19.0 - $19.5^{\circ}C$ by August, falling to approximately $8^{\circ}C$ in the following winter but then rising again to $12^{\circ}C$ by the end of the study in April 1975. Although there was considerable variation, temperatures recorded near low tide averaged 1 - $2^{\circ}C$ higher than those outlined above. Salinity during most of the year ranged from about 20 to 25 $^{o}/_{oo}$ at high tide to approximately 14 - 18 $^{o}/_{oo}$ at low tide. However, during the first two to three months of both 1974 and 1975, the salinity values were much lower, i.e. 10 and 15 $^{o}/_{oo}$ respectively. In contrast to the above values, Lloyd and Yonge (1947) reported maximum and minimum temperatures of 19 and $5^{\circ}C$ respectively for the Oldbury region while, in the case of salinity, their values frequently fell below the 14 $^{o}/_{oo}$ minimum recorded during most of this investigation.

The most common microscopic algae in the reservoir were diatoms and cyanophytes. The standing crop of these plants was always low, with maximum and minimum values of 1,000 and 100 cells l^{-1} occurring in the summer and winter respectively. On the other hand, the dry weight of suspended solids was relatively high, seldom falling below 1 g l^{-1} . The organic content of this material fluctuated between 4 and 18% of the total dry weight.

Taxonomy of Praunus and Gammarus

There has been some confusion over the taxonomy of both Praunus and Gammarus. For example, a number of instances in which the morphology of Praunus flexuosus (Müller) deviated from the key characters given by Tattersall and Tattersall (1951) are listed by Mauchline (1971b). The data obtained during the present investigation agreed with Mauchline, particularly with respect to the chromatophore arrangement, the colour of the setae on the antennal scale and uropods, and the shape of the telson cleft. However, close agreement was observed with Tattersall and Tattersall (1951) in the number of spines on the telson, i.e. greater than 21, and the shape of the antennal scale in which the length was always at least seven times as great as its width, characters which usually distinguished *P. flexuosus* from the closely related *Praunus neglectus* (G. O. Sars) (Mauchline, 1971b). Three aberrant specimens, with two to four spines at the end of the antennal scale rather than one, were collected during the present investigation, a situation paralleling that described by Holmquist (1957) for Scandinavian populations.

Both *Gammarus salinus* Spooner and *G. zaddachi* Sexton (Spooner) were distinguished from the *G. locusta* (L.) complex, from *G. oceanicus* Segerstrale and from *G. duebeni* Lilljeborg by the setation of the last segment of the mandibular palpus which has a ventral row of fringed setae in the first two species and an even row in the latter group (Kinne, 1954). The character used to distinguish *G. salinus* from *G. zaddachi* was the relative length of the setae to spines in the apical and subapical clusters on the hind margin of segment 4 of pereöpod 7 (Kinne, 1954; Segerstrale, 1959). Thus, in *G. salinus*, the hairs are shorter than the spines whereas in *G. zaddachi* the reverse is the case. While this character was always distinguishing, some of the others mentioned in the literature (Spooner, 1947; Kinne, 1954; Segerstrale, 1957, 1959), such as the number of spines on the urosome and the relative length and number of hair clusters on the segments of the peduncle of antenna 1 tended to display overlap (Table 35). Since it was not always possible to distinguish juveniles of *G. salinus* from those of *G. zaddachi* using just the above characters, animals representing these stages were examined using the additional methods of Dennert *et al.*, (1969). Thus, the ratio of the length of the setae to spines in the spical and subapical clusters on the hind margin of segment 5 of pereopod 7 was ascertained as also was the ratio of the greatest width of the basal segment of pereopod 7 to the mean length of the three longest spines. The values were always less than one in the former and greater than 8.5 in the latter, indicating that all the juveniles caught in this study belonged to *G. salinus*.

TABLE 35 Some characters normally used for separating *Gammarus salinus* and *G. zaddachi*. Values given in the literature are compared with the values obtained in the present study for five adult males of each species.

	No. of spines on urosome	No. of segments in accessory flagellum	Length of accessory flagellum / Length of peduncle segment 2 of antenna 1	Length of inner ramus of uropod 3 / Length of outer ramus of uropod 3	Ratio of the length of antenna 1 peduncle segments 1 to 2 to 3 to the length of the accessory flagellum	No. of hair groups on antenna 1 peduncle segments 1, 2 and 3
G. zaddachi (lit.)	19.5	4 – 7	0.80 – 1.00	0.72	100 : 89 : 51 : 74	5,6; 7; 4
Actual 8 mm	20	6	0.53	0.89	100 : 94 : 56 : 50	3; 6; 4
10 mm	23	6	0.94	0.74	100 : 82 : 67 : 77	2; 6; 3
12 mm	23	5	0.74	0.73	100 : 90 : 50 : 67	6; 7; 3
14 mm	27	5	0.63	0.85	100 : 81 : 53 : 51	4; 4; 3
16 mm	20	7	0.68	0.68	100 : 90 : 52 : 62	4; 8; 4
Mean	22.6	5.8	0.70	0.78	100 : 87 : 56 : 61	4; 6; 3
G. salinus (lit.)	24.0	5 – 8	1.00 – 1.30	0.83	100 : 82 : 43 : 92	4,5; 5; 2
Actual 8 mm	26	5	0.94	0.78	100 : 82 : 67 : 77	3; 4; 2
10 mm	36	5	0.73	0.78	100 : 82 : 48 : 60	2; 6; 3
12 mm	26	6	0.80	0.80	100 : 96 : 52 : 77	3; 6; 3
14 mm	27	6	0.84	0.77	100 : 90 : 51 : 76	3; 6; 3
16 mm	27	7	0.82	0.78	100 : 97 : 52 : 79	5; 6; 3
Mean	28.4	5.8	0.83	0.78	100 : 89 : 54 : 74	3; 6; 3

Mysidacea

The most common mysid collected from the intake current of the Power Station was Neomysis integer (Leach). This species occurred in relatively small numbers during the first part of the investigation (January) but its abundance subsequently increased sharply during June and July (Fig. 74). Thereafter, the population fell to almost negligible levels but showed some recovery during the autumn. Towards the end of the investigation, i.e. January - April 1975, the number of Neomysis was slightly higher than during the same period in 1974. Since the above trends were also clearly detectable in the samples taken directly from the reservoir, with density values ranging at different times of the year from 0 to 240 individuals m^{-3}, this highly seasonal pattern in abundance in the Severn parallels Scottish and European populations (Kinne, 1955; Jarvekulg, 1965; Wiktor, 1971; Mauchline, 1971c). Although the upsurge of Neomysis in Kinne's (1955) study was probably due, at least in part, to the recruitment of young, most of the specimens collected from the intake current in this study were adult. Thus Neomysis apparently swarms near shore in the Severn during the summer, as it also does in Scottish lochs (Mauchline, 1971c). Although the basis of this behaviour is not well understood, factors such as light intensity, weather and tidal conditions may play a key role in its timing and intensity (Jansson and Kallander, 1968; Mauchline, 1971c).

Although Neomysis occurred abundantly throughout the water column in the reservoir, a distinct vertical zonation was observed with respect to the size of the animals. For example, during July , when the numbers were at unusually high levels, the average length of specimens captured from the upper two meters of the reservoir was 7.5 mm, with extreme values of 4.0 and 14.0 mm. These figures may be compared with an average of 10.0 mm (range 6 - 18 mm) for the intake samples derived from the bottom of the water column. Similarly, during December when the standing crop was comparatively low, the Neomysis collection from the surface of the reservoir averaged 10.4 mm in length (range 6 - 15 mm) compared with a value of 12.6 mm (range 5 - 16 mm) for the bottom samples. Although the above data were collected under sunny conditions when the water was relatively calm, virtually the same pattern was observed in overcast weather with

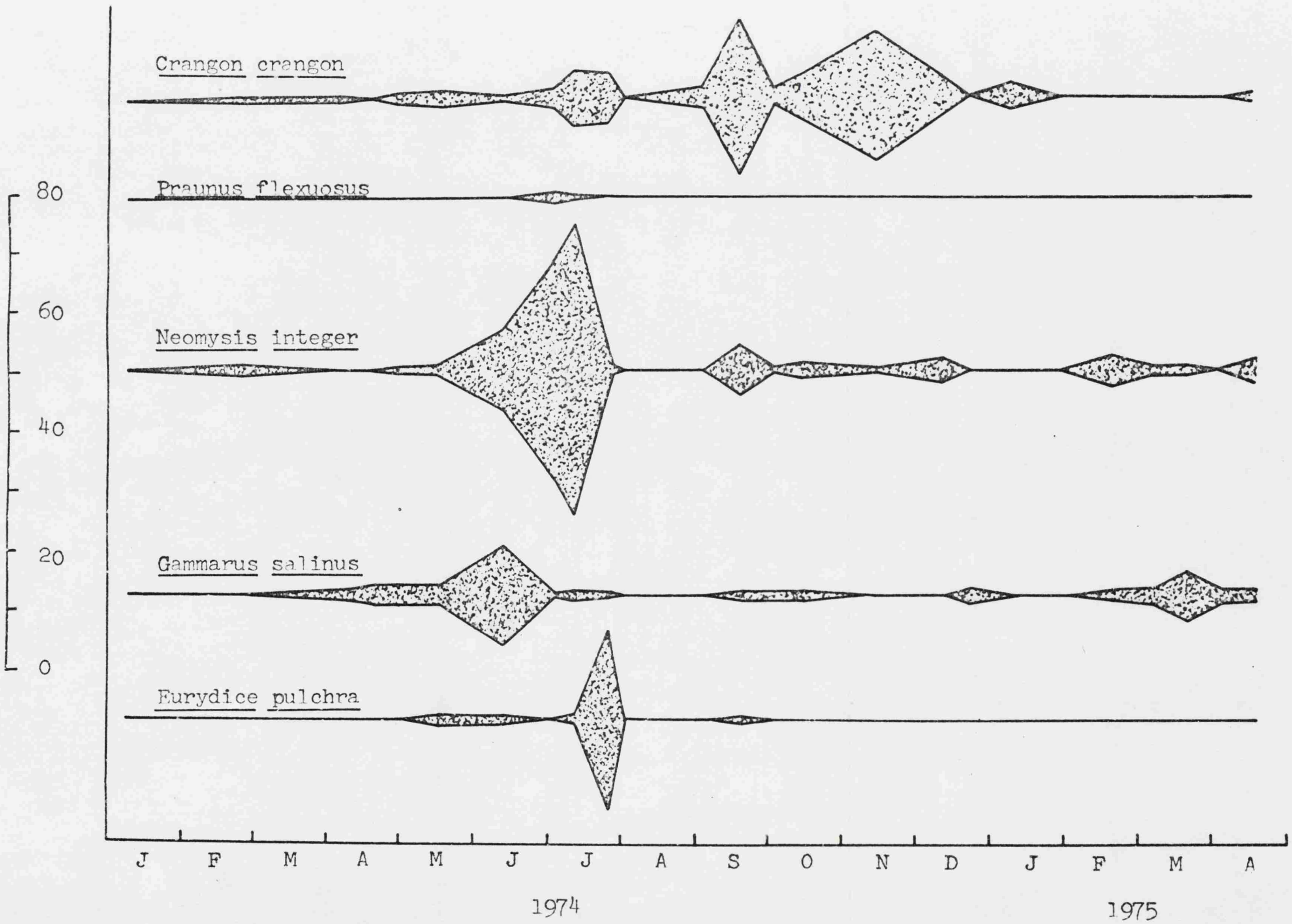

Fig. 74. Seasonal changes in the abundance of crustaceans collected from the cooling intake of the Oldbury Power Station. The scale represents the number of individuals collected per min.

waves measuring up to 0.5 - 0.7 m in height. Clutter (1967, 1969) reported that although in several different mysid species there was normally no segregation within the water column, the juveniles were found most frequently higher in the water column than adults during periods of vertical migration..

Since the different sized individuals of Neomysis exhibited a degree of vertical zonation, care must be exercised in considering samples as truly representative of the population either in the case of the intake or the reservoir samples. Furthermore, since tidal fluctuations in the Severn are exceptionally large, it is likely that Neomysis is carried considerable distances each day by the tide, thereby introducing the possibility that mixing takes place between groups of individuals which had previously been exposed to different environmental conditions. Thus, an estimate of the composition of the fauna in and around the reservoir will not be presented in detail as was done by Mauchline (1971a) in his study.

Females with eggs or young in the marsupium were collected from the intake current in all months except December 1974. During the colder months less than 2% of the females contained eggs or young, but this value rose to 10 - 15% in late March and to 60 - 80% in the spring. Thereafter, the levels fell gradually with the August values for example averaging only 10%. Specimens with empty marsupiums, i.e. those from which the young have recently emerged, on the other hand, were recorded throughout the year. Although the minimum size at maturity was 10 mm, large numbers of berried animals were not recorded until they had reached 13 mm. In general, females occurred more abundantly than males, usually representing 65 - 85% of the total catch. In certain instances, however, the males did account for nearly 50% of the haul, as was the case during the early part of December 1974. Young Neomysis, i.e. shorter than 2 - 5 mm, were recorded from the surface waters of the reservoir from May until December but appeared to be absent at other times. The maximum size of females was always larger than that of the males with the extreme lengths of the two sexes being 20 and 17 mm respectively.

From the above data it is clear that the composition of the mysid assemblage in the reservoir closely resembled that described by Mauchline (1971a, 1973) for populations living in Scottish lochs. Thus, as in Mauchline's study, breeding apparently occurred throughout the year, thus possibly producing three main generations, as has been noted in other parts of Europe (Vortsman, 1951; Kinne, 1955). The maximum length of Neomysis, 20 mm, exceeded the 17 - 18 mm limit found by Tattersall and Tattersall (1951) and Mauchline (1971a). This difference in length, together with the unusually high lipids in the Severn stocks (Moore, In prep.) suggests that growth conditions in the estuary are highly favourable for this species.

Praunus flexuosus was the only other common member of the Mysidacea collected at the Power Station. Except during July, this species usually occurred at relatively low densities (Fig. 74). Since, as with Neomysis, the pattern of seasonal change in abundance in the reservoir was almost identical to that recorded from the intake, with density values ranging from 0 to 10 individuals m^{-3} , this species apparently forms inshore aggregations during the summer. In contrast, Mauchline (1973) suggested that such behaviour in Scottish lochs was restricted primarily to December, while the relatively high numbers he recorded during the summer were due to the recruitment of young. Since in the present study the intake current sampled primarily the adult population, this could not have been responsible in this study for the increase in abundance during the warmer months. Blegvad (1922), working in Danish waters, recorded maximum numbers late in the summer and once again this pattern can be related to the appearance of young.

As with Neomysis integer the average and range in length of Praunus in the upper two m of the reservoir water column always tended to be less than that recorded in the samples taken from near the bottom. Thus, at the beginning of July, this species had a mean length of 14.0 mm (range 9 - 21 mm) in the surface waters while towards the bottom the corresponding value was 18.1 mm (range 11 - 25 mm). Although data are limited due to the relative scarcity of this species, weather and wave conditions apparently had little effect on vertical distribution.

Since Praunus was captured in large quantities only during June and July, an analysis of the composition of the population was restricted to this period. Females with eggs or young in the marsupium and collected from the intake, represented from 30 to 50% of the population. As, however, the smallest specimen captured during the investigation measured 9 mm in length, it would appear that the release of young does not take place in the reservoir. Females invariably outnumbered males in a ratio of at least 3:1 and the maximum length of these animals was 26 and 21 mm respectively. Mauchline (1971b) reported that most of the females in Scottish areas had eggs or young in the marsupium in June.

Calanoida

The only copepod recorded during the present investigation was Eurytemora affinis (Poppe). This species, which attained a maximum density of approximately 50 individuals m^{-3}, was taken in vertical plankton hauls only from the upper one m of the reservoir water column between the months of November 1974 and March 1975. Since Eurytemora generally prefers only slightly brackish water, its highly seasonal pattern of occurrence in the present investigation coincides well with the period of low salinity and high discharge from the rivers.

The entire collection of Eurytemora consisted of adults, with the percentage of males ranging from 31 to 61% (average 45%). In general, only 5 - 6 % of the females carried eggs but towards the middle of December this value increased to 80 - 85%. The average number of eggs on berried females was approximately ten with maximum and minimum values of 28 and two respectively, while the number of ovisacs averaged five and ranged from 0 to 26.

Although nauplii were never captured during the study, the presence of egg-bearing females clearly indicates that reproduction occurs during the winter. As with several other copepods (Marshall and Orr, 1955), breeding activity in Eurytemora probably takes place in well defined cycles, a point demonstrated by the high proportion of egg-carrying females at only one point during the study.

Isopoda

Eurydice pulchra Leach was the predominant isopod collected from the cooling intake of the Power Station. This species appeared to be rare during the colder months rising in abundance during May and June to a well defined peak towards the end of July (Fig. 74). As with the other organisms investigated, the seasonal trend exhibited in the reservoir plankton samples paralleled that observed in the intake current. Although Eurydice frequently occurs in intertidal sands at low tide (Crawford, 1937; Wolff, 1966; Naylor, 1967), no animals were captured from this habitat during the present investigation. However, a large number of specimens were found under rocks, particularly during the spring of 1975.

Since virtually all of the specimens of Eurydice collected from the reservoir measured less than 4 mm in length, the sharp rise in abundance of this species recorded during July was almost entirely due to the recruitment of young. In contrast to the above peaks in standing crop, Jones (1970a) found that in southern Wales Eurydice occurred most frequently near the first of September but once again this rise in abundance was due primarily to the appearance of young. Since water temperatures in the Severn were always several degrees higher than those in the study conducted by Jones (1970a), reproductive activity in Eurydice pulchra, which is highly limited below 10°C (Salvat, 1966), undoubtedly began several weeks earlier in the Severn, thus accounting for the difference in the timing of the appearance of the juveniles.

Eurydice exhibited a highly exaggerated pattern of vertical distribution in the reservoir. For example, during periods of high population density, i.e. July, large numbers of animals, 4 - 10 m^{-2}, were observed swimming at the surface of the water while 20 - 35 individuals m^{-3} were recorded in the upper one meter of the water column. These values may be compared with a maximum figure of about 10 animals m^{-3} from the bottom two meters of the reservoir. Unlike the mysids, Eurydice occurred towards the surface only under relatively calm conditions. In contrast to the above data, several authors (e.g. Jones et al., 1968) have indicated that Eurydice normally remains burrowed during the day, the reason for this difference probably lying in the fact that the level of illumination in the water column was greatly reduced by the large amount of suspended solids, a view previously suggested for Crangon by Lloyd and Yonge (1947).

Numerous estimates of the density of E. pulchra have been made in both Britain and Europe but since these determinations have been restricted to populations burrowed into the intertidal sand flats, comparisons with the planktonic data obtained in this study cannot be made. Although Eurydice may occur at densities of over 1,000 individuals m^{-2} in the substrate (Scott, 1960; Salvat, 1966; Jones, 1970a) few animals were captured from this habitat during the present investigation, a feature possibly attributable to its high organic content (Jones, 1970b; Jones and Naylor, 1970).

Amphipoda

Gammarus salinus Spooner was by far the most common amphipod collected from the intake current (Fig. 74). In general, this species was least abundant during the colder months but rose in numbers during the spring to reach a maxima in June. Precisely the same sort of pattern was exhibited in the reservoir samples with the standing crop occasionally approaching 85 individuals m^{-3}. On the intertidal flats outside the reservoir G. salinus was always plentiful under rocks.

The sharp seasonal rise in abundance of G. salinus described above coincides with the appearance of the young. Thus, during May the average length of Gammarus taken from the reservoir was 8.3 mm, with only 14% of the catch being under 5 mm in length. During June, however, the mean length of this species fell to 4.9 mm with 44% of the population averaging less than 5 mm.

As with the other species of crustaceans under investigation, a well defined vertical zonation with respect to the size of the animal was exhibited in the reservoir. Thus, in June, approximately 60% of the catch from the uppermost one meter of the reservoir consisted of specimens shorter than 5 mm compared with a value of 14% for the intake samples which, as previously mentioned, sampled the bottom layer of water. This pattern was also well illustrated by the fact that the maximum length of organism taken towards the surface (0.8 mm) was considerably less than the value obtained from the intake (15 mm). Since considerable difficulty was encountered in obtaining a representative cross section of the population living under the rocks in the intertidal zone, it is not possible to give an accurate assessment of the proportion of animals shorter than 5 mm. It is important to note however, that many specimens exceeded 15 mm in length, with a maximum value of 20 mm being recorded.

Detailed analyses of the composition of the population were conducted only between the months of September 1974 and April 1975. Although during this period, large numbers of animals were in the precopula stage, less than 5% of the females contained eggs. In contrast, Bassindale (1941), Spooner (1947) and Segerstrale (1950), working in a number of areas in Britain and Europe, reported that breeding was widespread during both March and April. Similarly, Segerstrale (1959) reported that reproductive activity in the closely related _Gammarus oceanicus_ Segerstrale reached maximum intensity between March and June while in northern France most female representatives of _Gammarus zaddachi_ were ovigerous by January (Dennert _et al._, 1969). Since unusually large numbers of young appeared in the intake samples towards the middle of June, the highest incidence of breeding in the Severn Estuary almost certainly occurred in May. This view is further substantiated by the fact that the maximum number of amphipods in the precopula stage were found during March and April. Since, however, amphipods measuring about 2 mm in length were taken in every month, breeding occurs throughout the year at a comparatively low level. The ratio of males to females measuring more than 8 mm in length fluctuated inconsistently during the investigation with maximum and minimum values of 5.5 : 1 and 0.6 : 1 respectively. Males were usually longer than females, representing for example 70% of the total catch in the length range 15 - 20 mm.

Callopius laeviusculus (Krøyer) was the second most abundant amphipod in the intake samples representing from 0.1 to 10% of the total amphipod catch. This species first appeared in the spring of 1974 reaching greatest abundance during the middle of July but thereafter decreasing in importance. In contrast to these changes in abundance, _Callopius_ was never taken in either the plankton samples from the reservoir or from the benthos. That this species was taken only from the bottom of the water column is presumably related to the fact that, since it is predominantly marine, it seeks out the region of greatest salinity. The earlier works of Bassindale (1941, 1942) indicated that, although _C. laeviusculus_ was very rare in both the

Bristol Channel and Severn Estuary, the closely related Callopius crenulatus Chevreux and Fage maintained a comparatively large population. Since this form was never recorded in the present investigation, environmental conditions in the estuary may have shifted to favour C. laeviusculus.

Bathyporeia pilosa Lindstrom occurred in both the intake and plankton samples in all seasons, but always at densities of less than 0.5 individuals m^{-3}, and was invariably absent from the substrate despite the fact that it frequently burrows (Watkins, 1939). Bassindale (1941) reported that B. pilosa was very rare in both the channel and estuary but others have frequently recorded it from the west coast of England and Wales. (Watkins, 1938; Fish and Preece, 1970).

Corophium volutator (Pallas) occurred most abundantly in the intake samples during June and July representing 5 - 10% of the amphipod catch at this time but was much less common in the spring and autumn and was totally absent in the winter. No animals were taken in the samples from the reservoir plankton and only one individual was recorded from the substrate. Despite its general scarcity in the present study, C. volutator is known to occur abundantly in other parts of the Severn Estuary as well as in the Bristol Channel (Boyden and Little, 1973). However, since the area outside of the reservoir is unsheltered and subject to considerable tidal flow, this factor was probably of considerable importance in limiting the abundance of Corophium (Spooner and Moore, 1963). As only large animals (greater than 4 mm) were captured from the intake, confirmation is provided for the laboratory observations of Meadows and Reid (1966) which indicated that young normally remained burrowed whereas the adults frequently swim.

Gammarus zaddachi was obtained only during February of both years when a total of ten individuals were caught. As this species generally prefers much less saline conditions than the closely related G. salinus, it occurs in greatest numbers high up in the estuaries (Dennert et al., 1969). Its appearance during February coincides with the period of lowest salinity values recorded during the investigation as well as a high discharge rate from the rivers.

Although Bassindale (1942) indicated that both *Marinogammarus marinus* (Leach) and *Hyale nilssoni* (Rathke) were relatively common in the area presently under investigation, only two representatives of each of these species were found during the present study. This points, as was the case with *Callopius laeviusculus*, to a relatively important change in the estuary during the last 35 - 40 years.

Orchestia gammarella (Pallas), a semiterrestrial amphipod (Wildish, 1970), always occurred in both the intake and plankton samples. Usually the standing crop of this species remained low, with the values for the plankton samples not exceeding 5 individuals m^{-3}. The population living along the beach of the study area consisted mostly of females which represented on the average 70% of the entire population (range 50 - 76%). No females with brood pouches were collected between September 1974 and April 1975, the only period for which these data were obtained. Amanieu (1967), working in France, found that for the months of September, October, March and April the proportion of females with brood pouches ranged from 4 to 70%.

Decapoda

Crangon crangon (L.) was by far the most common decapod collected during the investigation. The abundance of this species in the intake remained relatively low until July 1974 but then showed erratic increases reaching high levels in September and November but thereafter falling gradually to near zero levels (Fig. 74). The pattern of seasonal change in the abundance of *Crangon* collected in the vertical hauls from the reservoir almost exactly paralleled those outlined above with the density of these animals ranging from 0 to 75 individuals m^{-3}. No *Crangon* were collected from the substrate at either high or low tide, a surprising feature in view of the fact that it frequently burrows. As previously mentioned, however, the exceptionally high turbidity of the estuary has probably greatly reduced the need for concealment in the sediments.

The sharp reduction in the number of *Crangon* during the first few months of both years clearly indicates a migration out of the area. Since, as pointed out by Allen (1966) this species at low temperatures is not well to salinities of less than 15 $^{o}/_{oo}$, the animals must have moved down the estuary to the Bristol Channel. Much the same pattern was recorded by Lloyd and Yonge (1947) for the same area as well as by several other authors in different parts of England (e.g. Meredith, 1952). The gradual increase in the number of Crangon from May onwards suggests a movement back into the estuary with the elevated numbers in July being primarily due to the appearance of young (Fig. 75). The considerable fluctuation in the number of animals between August and November is probably a result of movements in search of food (Havinga, 1930; Meyer-Waarden and Tiews, 1957).

Males normally represented only from 3 to 13.5% of the entire catch above 20 mm. During February, March and June however, the proportion of males in the size class 20 - 45 mm increased to approximately 40% while the corresponding value for animals greater than 45 mm remained low, i.e. 6.5 - 12.0%. Since, however, only a few specimens were captured during these three months, the data obtained may not accurately represent the population. Although Lloyd and Yonge (1947) found a relatively greater amount of males in their samples from the Severn, Tiews' findings (1970), which indicated that commercial catches of Crangon made in Europe consisted almost exclusively of females, agree with the data obtained in this study for the largest animals.

The length distribution of female Crangon collected from the intake remained relatively constant between February and May 1974 (Fig. 75), the average length of the population varying from 43 to 46 mm (range 29 - 57 mm). During June, however, large quantities of young with an average length of 14 mm (range 8 - 21 mm) appeared in the catches at a time when the adults were becoming increasingly rare. Since the number of females carrying eggs increased sharply in May spawning clearly takes place at about this time. The young subsequently grew quickly, the average length of the population increasing to 35.5 mm by August and 44.5 mm by December.

Scarcely any female Crangon were captured from the intake which measured more than 60 mm (Fig. 75), an observation contrasting with the situation in Lloyd and Yonge (1947) which indicated over 25% of the population exceeded this length. In addition, the largest

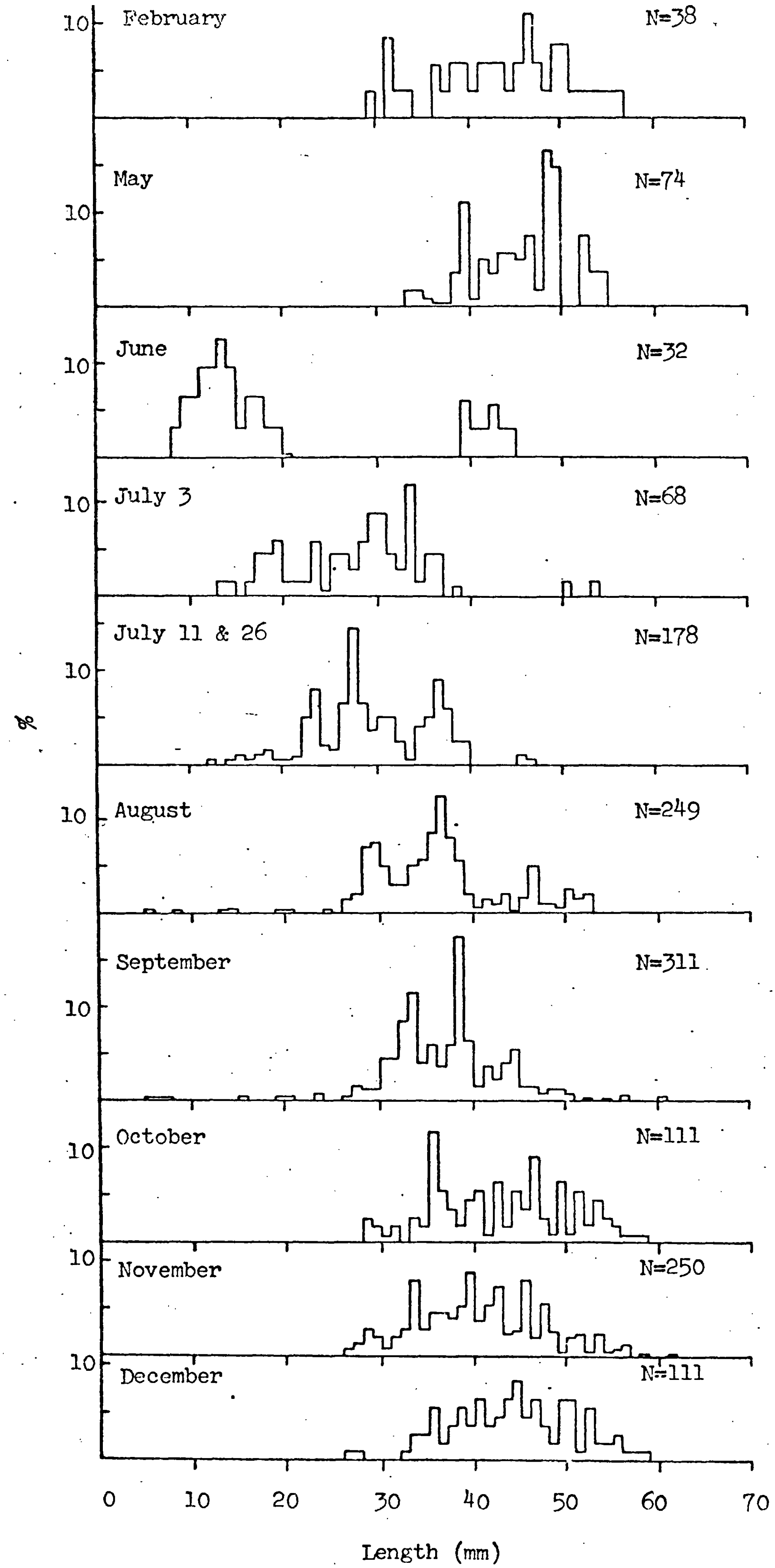

Fig. 75. The length distribution of female representatives of Crangon Crangon collected from the Oldbury Power Station at different times of the year.

specimen recorded during this investigation , 69 mm, was much smaller than the corresponding values of 85, 91 and 95 mm given respectively by Lloyd and Yonge, Havinga (1930) and Tiews (1954). Similarly, the largest males measured 58 mm in length compared with respective values of 72, 75 and 68 mm outlined by the above authors. In order to compare the Oldbury data with material collected elsewhere in the estuary, several samples of Crangon were collected from the Power Station at Berkley, which is situated a few kilometers upstream from the reservoir and draws water directly from estuary. As illustrated by the October 1974 data (Fig. 76), the average length of the population at Berkley was approximately 10 mm greater than that obtained from Oldbury at the same time with the longest female measuring 71 mm.

The minimum size at maturity in specimens from the intake, determined from the relative length of the raking setae on the first pleopod (Lloyd and Yonge, 1947) as well as the size of the ovary (Meredith, 1952), was 37 mm with virtually all specimens reaching this stage of development by 42 mm. Lloyd and Yonge, on the other hand, reported that Crangon was not mature until it had reached approximately 50 mm while, in European populations, the values ranged from 37 to 52 mm (see Tiews, 1970).

Berried females were captured in all seasons. During the winter, for example, between five and 20% of the specimens over 50 mm in length contained eggs while in the spring, summer and autumn, the corresponding values averaged 70, 30 and 15% respectively. Although these data contrast with the findings of Lloyd and Yonge obtained from the same location, numerous authors have reported the presence of berried females throughout the year in other parts of England as well as elsewhere in Europe (Havinga, 1930; Meyer-Waarden, 1935; Meredith, 1952). It should be noted, however, that the time when the number of berried females reached a peak in this study agreed with Lloyd and Yonge.

As with most of the other species under investigation, there was a distinct vertical zonation in the water column with respect to the size of the animal. Thus, during July for example, the average length of Crangon collected from the upper one meter of the reservoir was 16.5 mm (range 5 - 34 mm) while in the intake current, which sampled

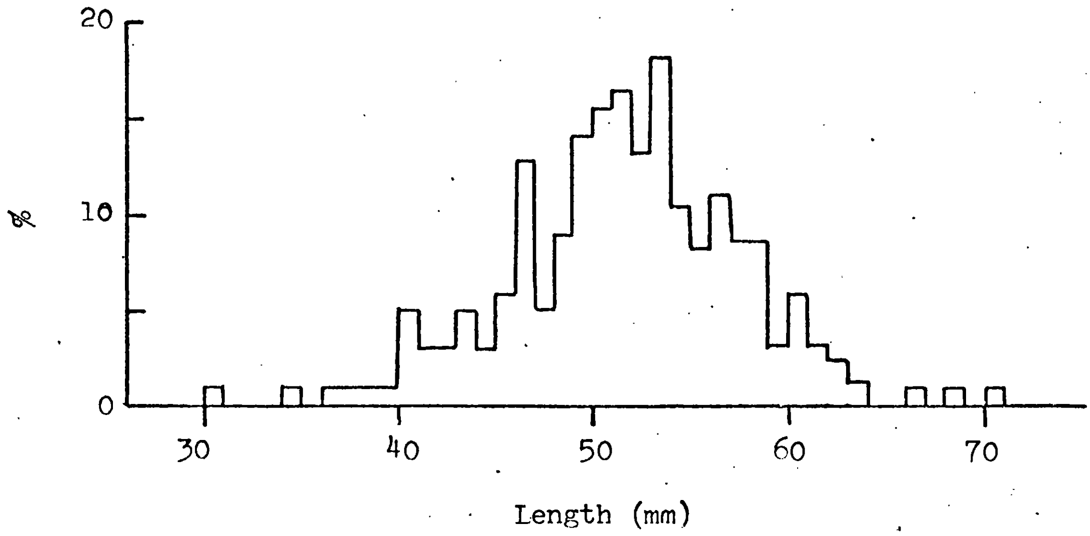

Fig. 76. The length distribution of female representatives of Crangon Crangon collected from the Berkley Power Station during October, 1974.

the bottom of the reservoir, the corresponding value was 29 mm (range 13 - 47 mm). In contrast Meyer-Waarden and Tiews (1957) and Plett (1965) found that young *Crangon* were absent from surface waters, and as pointed out by Tiews (1970), this pattern of distribution is probably not related to either temperature or salinity.

9. The Basis of Food Selection in some Estuarine Fishes

Introduction

Since the diet of many fish species often varies considerably with locality (Wheeler, 1969; Lythgoe and Lythgoe, 1971), inconsistent and highly variable patterns of food consumption have frequently appeared in the literature. It is thus difficult to make predictions of the type of food likely to be consumed by fishes in different environments. As comparatively few studies have analyzed the importance of many of the factors influencing the feeding biology of fishes, the present study gives details on those which may effect the selection of prey by several teleosts in the Severn Estuary.

Materials and Methods

Fifteen to twenty individuals of each fish species were collected every two weeks during 1974 from the cooling intakes of the Oldbury - on - Severn Power Station. They were immediately transported to the laboratory where their stomach contents were sorted, identified and dried by sublimation to constant weight. In addition, the wet weight, fork length and mouth dimensions (Keast and Webb, 1966) of the whole animal were recorded.

A number of flounders (average length 8.2 cm; range 4.0 - 15.8 cm), collected from the reservoir during April and May, were held in 140 l tanks supplied with estuarine water to a depth of 40 cm. Temperatures were kept at 12.0°C (range 11.5 - 12.5°C) while the photoperiod paralleled natural conditions. Light intensity at the surface of the water was 150 lux. Bottom deposits consisted of fine sand and the turbidity of the water was maintained at 2 - 3 JTU for one group of fish and 85 - 90 JTU for another. All the animals were fed to satiation every second day on the freshwater isopod *Asellus aquaticus*. After this acclimation period (30 days), food was withheld from the fish for four days. Using forceps, individual isopods of different sizes were then placed in the water. The greatest distance the fish could detect this organism and the time taken in swimming to it was recorded both in clear (2 - 3 JTU) and in turbid (85 - 90 JTU) water. Each fish was fed 3 - 5 isopods per experiment depending on the size of prey. Similar experiments were conducted using the amphipod *Gammarus pulex*, the decapod *Crangon crangon*, the isopod *Eurydice pulchra* and the mollusc *Macoma balthica*.(L.). After the acclimation and starvation periods, a second group of fishes were presented with *Gammarus pulex* and *G. salinus* which have dark green-grey and light tan colouration respectively. The greatest distance the fish detected these two prey species and the time spent in swimming to them in both clear and turbid water was again recorded.

Results

Flounders, Platiohthys flesus (L.)

Since most of the flounders captured during the winter contained little or no food in their stomachs, the data collected at this time are not included. The stomach contents of flounders, measuring 6.0 - 35.0 cm in length and captured between February and October, consisted mainly of Gammarus salinus, Neomysis integer and Praunus flexuosus, irrespective of the size of fish (Fig. 77). Representatives of Crangon crangon, Corophium volutator, Eurydice pulchra and Nereis diversicolor (Müller), although normally of little importance, were occasionally ingested in relatively large quantities. In terms of numbers, the relative abundance of ingested Gammarus remained comparatively stable at about 40% of the total stomach contents, but then decreased more or less continuously to approximately 5% in September, only to rise again to 35% in October. As illustrated in Fig. 78 , these values are, to a large degree, lower than those recorded from the reservoir intake samples, a feature which is particularly striking considering Gammarus occurred abundantly near the bottom, regardless of tidal condition, where flounders are normally found. However, large quantities of this species were concealed among floating weeds and debris making them unavailable to the fish. Thus, in terms of accessible prey, Gammarus was probably consumed in roughly the same proportion as it occurred in the environment.

The amount of Neomysis ingested by the flounders increased more or less continuously from 12% of the total stomach contents in February to approximately 80% in August and September but fell to only 20 - 25% in October. Thus, although this pattern of change bears little relationship to seasonal fluctuations in the reservoir (Fig. 78) a certain degree of selection was still detectable for this species. Part of the preference for Neomysis must have occurred as a consequence of the selection against Gammarus salinus. Thus, as this latter species was eaten in unusually small quantities, all other organisms must have been ingested more frequently than they occurred in the environment. Furthermore, since Neomysis was relatively immotile it would have been unable to escape predation and it was

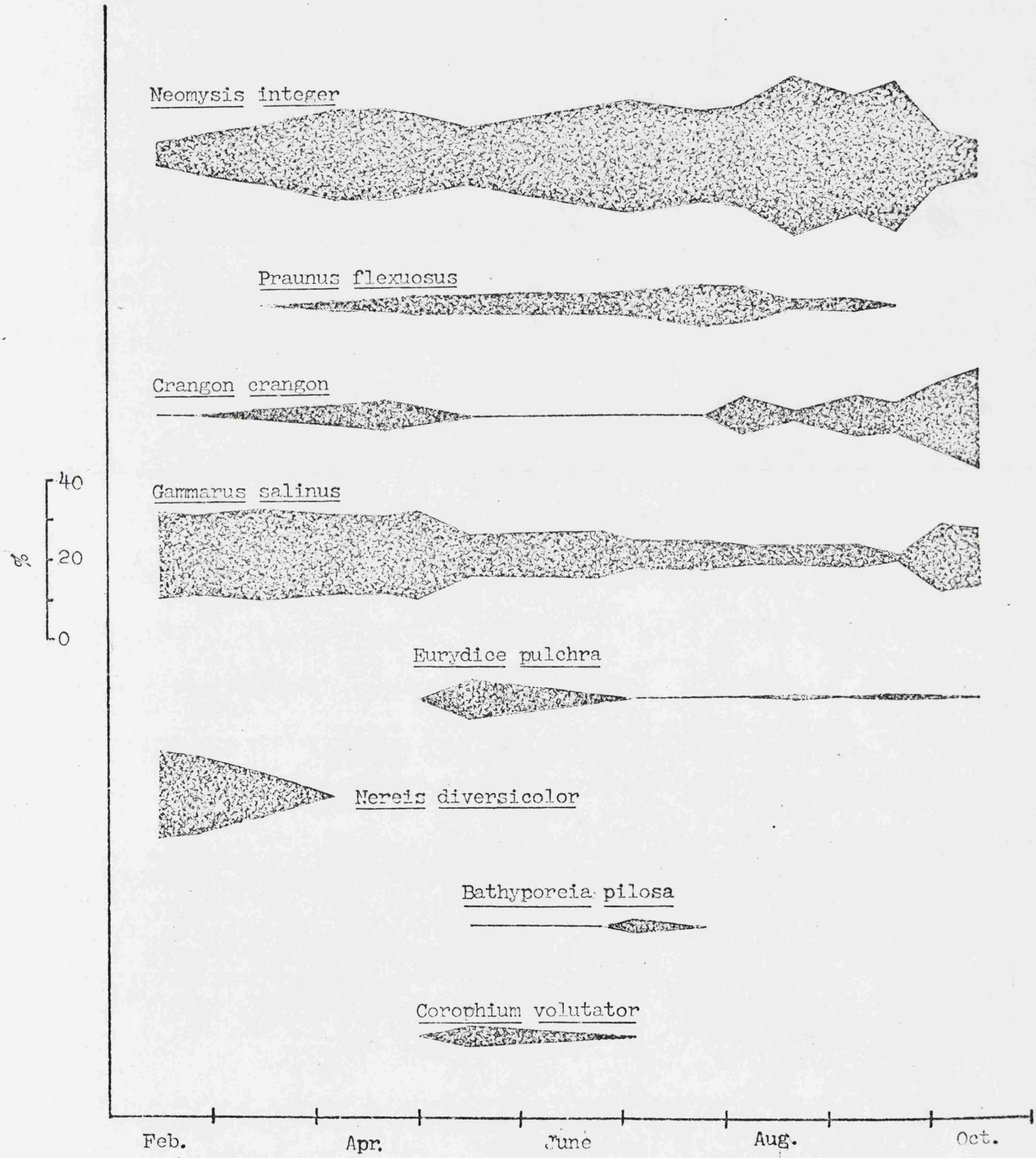

Fig. 77. Species composition of the stomach contents (expressed as a percentage by numbers) of flounders longer than 6.0 cm collected from the Oldbury reservoir.

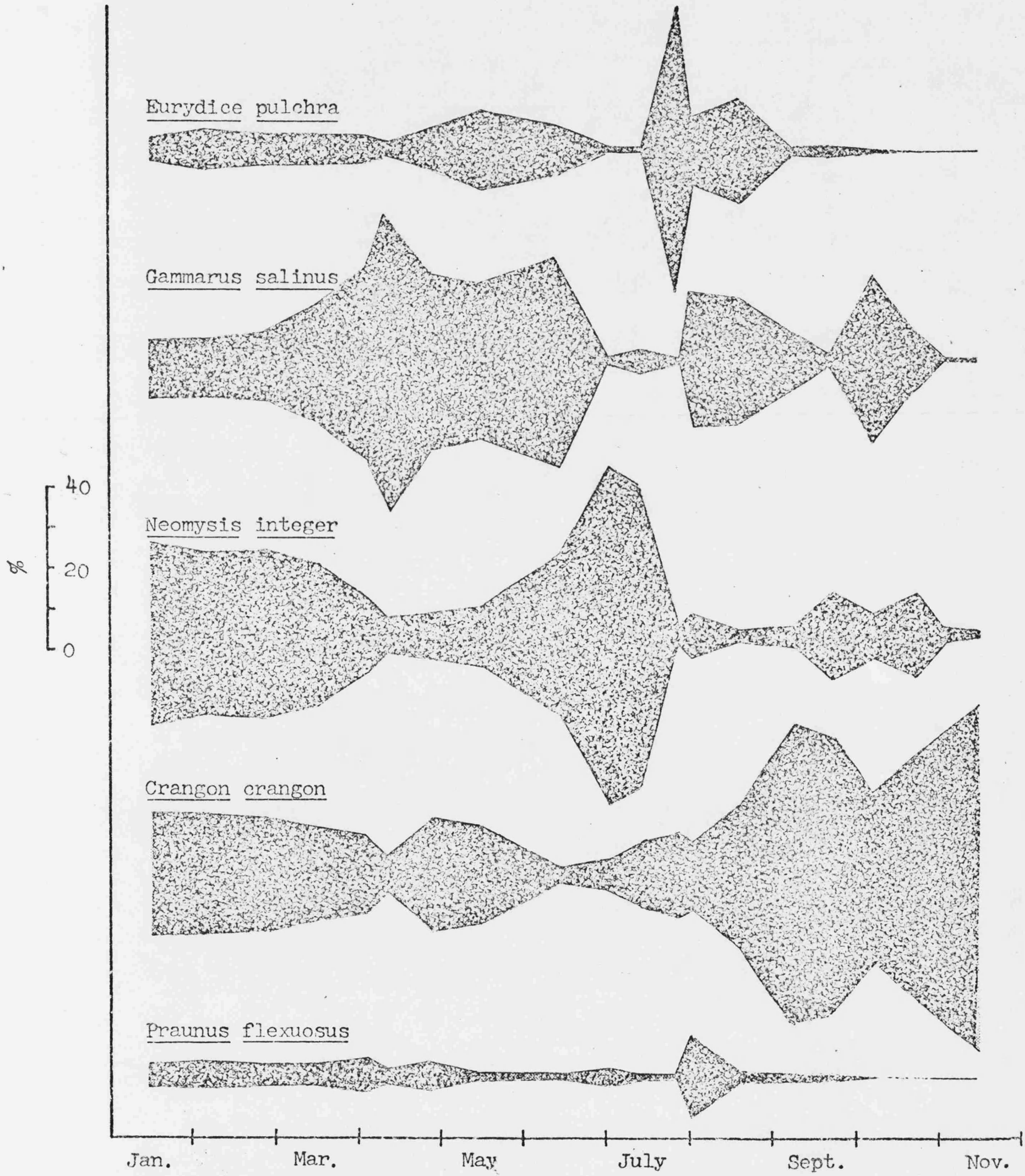

Fig.78. The relative abundance of organisms collected from the cooling intake of the Oldbury Power Station at different times of the year expressed as a percentage of total numbers.

never found concealed among weeds or debris. During April/May and August/September, Neomysis occurred in comparatively small numbers in the reservoir but continued to be predominant in the stomach. In the months prior to these two depressions, large populations occurred in the reservoir. It is thus possible that the fish had become accustomed to eating Neomysis and would exhibit a preference for it during periods when the standing crop was low. Yet, as demonstrated in laboratory experiments,such feeding behaviour is usually not exhibited by flounders. A more plausible explanation for the marked selection for this species may lie in the fact that, apart from Gammarus and a few other comparatively rare forms, no other prey were available, either because they were of unsuitable size or because they occurred in an essentially inaccessible part of the water column. These points are given further consideration later in the text.

Flounders seldom ate Crangon crangon, even though this species was common, at least at low tide, near the bottom of the reservoir. Its scarcity in the gut can probably be attributed, in part, to size selection and also, as discussed later, through its unique escape reaction. The possibility also exists that water temperatures during the summer were too high for optimal hunting and thus the fish may have had considerably greater difficulty in catching such motile prey at this time. However, as demonstrated in laboratory experiments, the ability of flounders to catch C. crangon remains virtually unchanged between 12 and 25°C , temperature cannot be important in selection. October was the only month in which Crangon was frequently ingested, when it accounted for 40% of the total contents. Its predominance in the stomachs at this time can undoubtedly be attributed to the comparative rareness of other potential prey species and the fact that most representatives of Gammarus salinus were too small for consumption (page 125). This feature can also, but to a lesser degree, be applied to Neomysis integer. Eurydice pulchra was also consumed in small numbers, a pattern presumably related to the fact that virtually all individuals were often found much higher in the water column than the fish. At low tide each species occurred together but the rapid movements of Eurydice resulted in an unusually brief contact time for the flounders to capture this prey (page 143).

Although a large number of burrowing polychaetes, mainly Nereis diversicolor, occurred in the sediments of the reservoir and surrounding area, the flounders seldom utilized this food source, contrasting with the results reported by several other authors working on a variety of flatfish species (Richards, 1963; Miller, 1967; Pitt, 1973; Wells et al., 1973). This discrepancy with other studies is undoubtedly due to the presence of great numbers of suitable non - burrowing prey in the reservoir. During February , however, Nereis diversicolor did represent 30 - 44% of the total stomach contents, a feature probably due to the fact that, at low temperatures, flounders are able to catch only sedentary prey (page 144) and reflecting the influence of cold temperatures on metabolic rate (Mulicki, 1947). Molluscs, present in only small numbers in the environment, were never eaten. In contrast, such prey is frequently consumed in large numbers by flounders (Jones, 1952) and other flatfishes (Kennedy and Steele, 1971; Tyler, 1972). As demonstrated in laboratory experiments flounders living in this part of the Severn Estuary have apparently become conditioned to eating softer-bodied prey.

In terms of dry weight, Crangon crangon formed by far (> 70%) the most important part of the diet of flounders longer than 6.0 cm during April and from August to October but, at other times, was of only minor significance. Nereis diversicolor was most important early in the study representing up to 63.5% of the stomach contents. Praunus flexuosus occurred most abundantly in the stomachs between May and July, accounting for 48 - 63% of the total contents. Neomysis integer invariably ranked second in abundance at this time (24 - 38%), followed by Gammarus salinus (5 - 10%) and Eurydice pulchra (0 - 8%). The overwhelming predominance of Crangon in the stomach for part of the study at least parallels their abundance in the reservoir. Thus, the fish fed most heavily on the species which could withstand the greatest amount of predation. Since comparatively rare organisms were utilized during the three summer months when Crangon was of little importance, the fish may have significantly reduced the standing crop of these less common species.

The average length of Gammarus salinus in the stomachs of flounders longer than 6.0 cm usually exceeded 1.2 cm. In contrast, specimens collected from the reservoir intake averaged only 0.5 - 1.0 cm . This selection for large individuals is particularly striking considering the longest organism ingested by the fish (1.7 - 1.8 cm) was greater in size than those taken from the inflow samples. Much the same pattern was exhibited for Neomysis integer, although the differences in length were usually not as sharp as those exhibited for Gammarus. On the other hand, only the smaller representatives of Crangon crangon were eaten by the fish. For example, the average length of this species in the stomachs during April was 3.7 cm compared with 4.5 cm in the reservoir. Similarly, the corresponding values in August were 2.8 and 4.2 cm respectively. Only the largest representatives of Eurydice pulchra (0.5 - 0.7 cm) were eaten. In contrast, little size selection was exhibited for Praunus flexuosus, a point exemplified by the fact that the length of ingested specimens during May and July averaged 2.5 and 1.4 cm respectively, values which are virtually identical to those found at these times in the environment.

Selection for a particular size of organism has been reported on numerous occasions for a wide variety of fishes (Shelbourne, 1962; Lawler, 1965; Chilvers and Gee, 1974). In the present study, flounders restricted themselves to small specimens of Crangon, presumably because of the limitations of mouth size. In addition, large animals could probably escape from this predator with little difficulty. Both of these points are given further consideration later in the text. The absence of small Gammarus from the stomach can undoubtedly be attributed to the difficulty the fish had in detecting these organisms in the turbid water. Although some variation existed, the smallest representatives of Neomysis integer and Eurydice pulchra eaten by the fish were comparable in size to ingested Gammarus. Once again, it seems likely that considerable difficulty existed in seeing these smaller organisms. Little if any selection was exhibited for Praunus flexuosus of different size, a feature presumably attributable to the fact that their size always fell within the size range of organisms ingested.

The average length of ingested organism remained constant as the fish increased in size. During April, for example, specimens of Neomysis integer found in the stomachs of flounders measuring 5.0-7.0 cm averaged 1.19 cm in length while the corresponding value for fish longer than

20.0 cm was 1.11 cm. This contrasts with the situation observed in many other fishes which often ingest larger objects as they increase in size (Ivlev, 1961; Reshetnikov _et al._, 1972). As a wide range of prey was available in the present study, it seems likely that this aspect of the feeding biology of flounders is independent of size of fish.

The maximum length of frequently ingested organism increased from 2.5 cm in specimens measuring 6.1 - 10.0 cm to 7.0 cm in those of 15.0 - 20.0 cm (Table 36). However, since the longest prey eaten, _Anguilla anguilla_, was exceptionally narrow and flexible, its total length cannot really be compared with that of the ingested crustaceans. Excluding this organism, the longest prey consumed by flounders 15.0 - 20.0 cm in length was _Crangon crangon_ which measured 4.0 cm. Expressing the above data (using _Crangon_) as a percentage of fork length gives averages of 33 and 23% for the two size classes. These values are in agreement with those given for freshwater (Popova, 1967; Lewis, 1974), marine (Reshetnikov _et al._, 1972) and estuarine predators (Moore and Moore, 1974). The decline in the relative size of the flounder's prey parallels changes in mouth morphology (Table 37). The length of ingested elvers (_Anguilla anguilla_) accounted for approximately 40% of the fork length of large flounders. The frontal area of this prey was considerably smaller than that of most ingested crustaceans and thus there were probably no restrictions imposed by mouth size. As _Anguilla_ is highly flexible, it can be easily coiled within the flounder's comparatively small stomach.

The minimum size of frequently ingested prey increased from 0.6 cm in fish measuring 6.1 - 10.0 cm in length to 0.9 cm for specimens of 15.0 - 20.0 cm (Table 36), values considerably higher than those reported by Mulicki (1947) for flounders in another region. As mentioned earlier, however, this species is probably unable to catch small prey in turbid water.

The percentage of stomachs that contained no identifiable remains decreased from approximately 80% in December to 55 - 60% between January and March, but then increased to 90% in April (Fig. 79). Thereafter, values fell to about 60% in June but gradually rose to 96% by November. The changing proportion of non-feeding animals between April and November corresponds to fluctuations in water

Table 36. The maximum and minimum length of organisms found in the stomachs of fishes of different size collected from the Severn Estuary.

Flounder

Size Class (cm)		Organism	Average Length (cm)
0.0 - 6.0	Max.	*Gammarus salinus*	1.4
	Min.	*Corophium volutator*	0.4
6.1 - 10.0	Max.	*Praunus flexuosus*	2.5
	Min.	*Corophium volutator*	0.6
10.1 - 15.0	Max.	*Crangon crangon*	2.8
	Min.	*Neomysis integer*	0.9
15.1 - 20.0	Max.	Elver (*Anguilla anguilla*)	7.0
	Min.	*Neomysis integer*	0.9

Eel

Size Class (cm)		Organism	Average Length (cm)
15.0 - 25.0	Max.	*Crangon crangon*	3.0
	Min.	*Gammarus salinus*	0.3
25.1 - 35.0	Max.	*Crangon crangon*	3.4
	Min.	*Neomysis integer*	0.5
35.1 - 45.0	Max.	*Crangon crangon*	6.0
	Min.	*Neomysis integer*	1.1
45.1 - 55.0	Max.	*Crangon crangon*	6.5
	Min.	*Neomysis integer*	1.1

Whiting

Size Class (cm)		Organism	Average Length (cm)
2.5 - 5.0	Max.	*Neomysis integer*	1.4
	Min.	*Eurydice pulchra*	0.2

Table 36. (cont'd)

Whiting

Size Class (cm)		Organism	Average Length (cm)
5.1 - 7.5	Max.	*Pomatoschistus minutus*	2.5
	Min.	*Gammarus salinus*	0.25
7.6 - 10.0	Max.	*Pomatoschistus minutus*	2.8
	Min.	*Gammarus salinus*	0.2
10.1 - 12.5	Max.	*Crangon crangon*	3.9
	Min.	*Gammarus salinus*	0.25
12.6 - 15.0	Max.	*Gammarus zaddachi*	0.2
	Min.	*Crangon crangon*	5.4

Sprat

2.5 - 5.0	Max.	*Neomysis integer*	1.2
	Min.	*Gammarus salinus*	0.2
5.1 - 7.5	Max.	*Neomysis integer*	1.3
	Min.	unidentified amphipod	0.1
7.6 - 10.0	Max.	*Neomysis integer*	1.5
	Min.	*Gammarus salinus*	0.25

Table 37. Relative mouth dimensions, expressed as a percentage of fork length, in fishes of different size collected from the Severn Estuary.

Size Class(cm)	Width	Height
	Flounders	
0.0 - 6.0	4.8	5.0
6.1 - 10.0	4.7	4.8
10.1 - 15.0	4.0	4.8
15.1 - 20.0	4.0	4.6
	Eels	
15.0 - 25.0	2.9	2.4
25.1 - 35.0	2.7	2.2
35.1 - 45.0	2.5	2.0
45.1 - 55.0	2.4	1.9
	Whiting	
2.5 - 5.0	7.7	12.5
5.1 - 7.5	7.5	12.3
7.6 - 10.0	6.1	10.0
10.1 - 12.5	6.0	9.8
12.6 - 15.0	5.8	9.7
	Sprat	
2.5 - 5.0	4.2	13.0
5.1 - 7.5	4.0	12.0
7.6 - 10.0	3.8	10.1

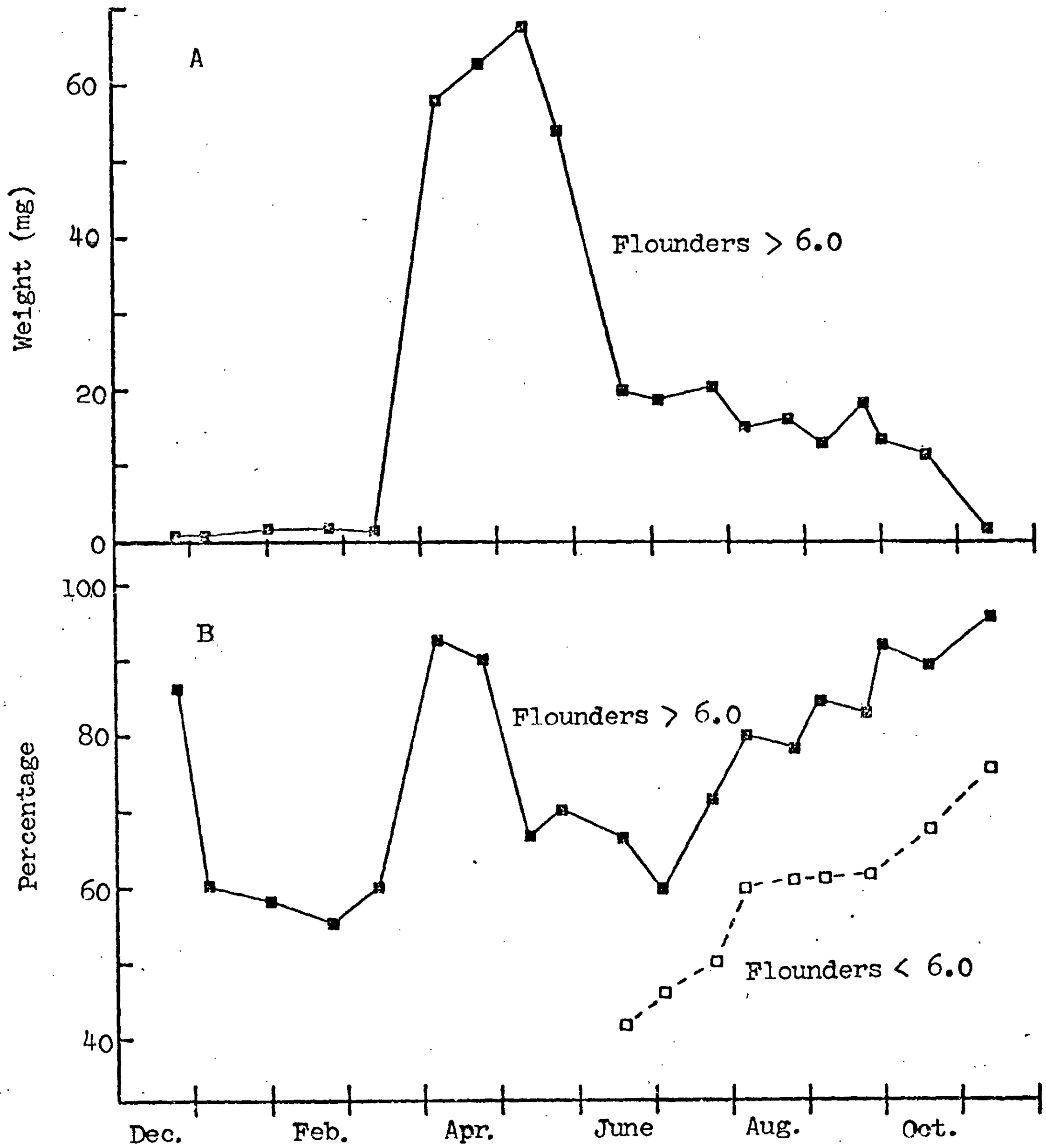

Fig. 79. Changes in the dry weight of stomach contents (A) and the percentage of stomachs which contained no identifiable remains (B) in flounders of different size collected from the Oldbury reservoir.

temperatures, a point already noted by Mulicki (1947) for the same species. However, between January and March, values averaged only 55 - 60% even though water temperatures remained low, i.e. 7 - 8°C. Since there was no significant change in any of the other environmental parameters measured at this time, the reason for this variation remains unknown. The pattern of change in non-feeding animals was, to a large degree, the reverse of variations in the standing crop of organisms in the reservoir (page 115). The proportion of feeding flounders is thus , as previously suggested by Mulicki (1947), apparently dependent on the amount of food present in the environment. Prey remained, however, comparatively abundant even during periods of low standing crop. It therefore seems likely that these organisms were always readily available and the fish had little difficulty in catching them. However, as the estuary was always exceptionally turbid, the fish probably had problems in finding prey more than a few centimeters away, a restriction which would have greatly reduced availability. In addition, the more motile species, even though detected by the fish, could have easily escaped, particularly in the turbid water. The importance of these points in the feeding biology of flounders is emphasized in laboratory experiments(page 142). The proportion of empty stomachs was relatively high compared to other fishes(Mulicki, 1947; Tyler, 1971).

The weight of stomach contents varied considerably during the study (Table 38 , Fig. 79). During February , March and November, 50 g fish contained about 1.5 mg of food in their stomachs with the value rising to 50.6 mg during April and May, only to fall again in June/July and August/September to 19.8 and 15.0 mg respectively. Since water temperatures in the reservoir averaged 7 - 8°C during both February/March and also in November they were too cool for active hunting and digestion (Mulicki, 1947). The dramatic rise in the weight of the stomach contents during April and May was probably due to the fact that water temperatures were sufficiently high to allow active hunting but remained too low for comparably rapid digestion. Such a point has been made for several other species (Tyler, 1971) and is supported by the fact that flounders held in the laboratory fed actively at temperatures comparable to those in the reservoir during April and May. As the weight of stomach contents fell during

Table 38. Monthly changes in the dry weight of stomach contents (mg) for fishes of different weight (g, wet) collected from the Severn Estuary expressed as a logarithmic regression (Log Y = a + b Log X).

Month	Sample Size	Average Fish Weight (range), g	a	b	r
Flounders > 6.0 cm					
January,February,November	37	72.1 (10.3 - 179.9)	-0.5873	0.4454	0.69
March,April,May	40	25.8 (5.0 - 137.6)	0.0313	1.0264	0.72
June,July	20	60.1 (5.6 - 144.0)	-0.6800	1.1634	0.71
August,September,October	26	39.8 (8.8 - 99.1)	-1.2268	1.4165	0.75
Flounders < 6.0 cm					
July	26	0.8 (0.4 - 1.2)	1.2951	4.1004	0.85
August,September,October	39	1.4 (0.9 - 3.1)	1.1262	1.9694	0.82
November	17	1.5 (1.0 - 6.3)	0.1605	0.7077	0.71
Eels					
April,May	17	62.2 (9.6 - 135.7)	-1.8774	2.3721	0.88
June-October	52	92.5 (18.3 - 230.0)	0.5585	0.8450	0.76
Whiting					
December(1973)-March; August-November	287	4.34(0.6 - 26.7)	0.1063	2.1653	0.81
Bib					
December(1973)-March; August-November	97	7.62(1.3 - 24.6)	0.4761	1.4692	0.86

Table 38. (cont'd)

Poor Cod

Month	Sample Size	Average Fish Weight (range), g	a	b	r
December(1973)-March; August-November	113	4.98(1.4 - 22.0)	0.1164	2.0043	0.76

the summer months and the temperatures averaged 15 - 18°C , digestion may have improved. The possibility also exists, however, that the comparatively warm water had caused a reduction in feeding intensity. Flounders captured between May and October contained considerably less food in their stomachs than most other northern temperate zone fishes (Tyler, 1971). This feature, together with the high percentage of empty stomachs and comparatively slow growth rate, suggests the species has considerable difficulty in finding food in this part of the estuary.

Most fishes exhibit daily fluctuations in feeding intensity associated with such factors as time of day (Keast and Welsh, 1968) and tidal state (Healey, 1971). In the present study, the degree of freshness of ingested material and the weight of stomach contents showed little correlation with changes in environmental parameters a pattern reported on at least one other occasion for another species (Moore and Moore, 1974).

The diet of flounders shorter than 6.0 cm consisted almost entirely of *Neomysis integer, Gammarus salinus* and *Corophium volutator*. During July, when the fish first appeared in the reservoir, *Neomysis* accounted for approximately 66% by numbers of the ingested material, followed by *Gammarus* (20%) and *Corophium* (14%). The relative abundance of *Neomysis* increased during August to 82% while that of *Gammarus* and *Corophium* fell to 10 and 8% respectively. By September and October, the abundance of these organisms averaged 78, 10 and 5% respectively. Few fish contained food in their stomachs during November and thus the data obtained at this time do not warrant description. Similarly, scarcely any fish shorter than 6.0 cm were captured during the earlier part of the study.

As with large flounders, *Neomysis* occurred more abundantly in the stomach than in the intake samples while the opposite pattern existed with *Gammarus*. Presumably, the basis of this selection was similar to that outlined for the larger fish. Small flounders never ate *Praunus flexuosus, Crangon* and *Eurydice*. The absence of the first two species from the stomach contents can undoubtedly be attributed to size selection. For example, the largest organism (1.4 cm) ever ingested by the fish (Table 36), approached the minimum size of

Praunus and Crangon in the reservoir. In addition, as demonstrated in laboratory experiments, small flounders probably had extreme difficulty in catching these organisms, as was also the case with Eurydice pulchra. The change in the diet of flounders at 6.0 cm , although remarkably sharp, is generally characteristic of juvenile fishes (Carr and Adams, 1973).

In terms of dry weight, Neomysis integer always accounted for more than 63% of the stomach contents, followed by Gammarus salinus (25 - 31%) and Corophium volutator (4 - 6%) (Table 38). Crangon crangon and Praunus flexuosus, although frequently predominant in the stomachs of large flounders, seldom represented more than 1.0% of the total contents.

Both the average(1.0 - 1.2 cm) and maximum (1.8 cm) length of ingested Neomysis corresponded to those in the environment. However, the smallest ingested specimen, 0.8 cm, measured approximately 0.2 cm longer than that of the available stock. Although some variation existed, ingested representatives of Gammarus salinus were usually larger than those present in the intake samples, with average values of 0.7 - 0.9 and 0.4 - 0.5 cm respectively. The extremely large individuals eaten by flounders greater than 6.0 cm were never taken, presumably because of relative mouth dimensions (Table 37). Corophium volutator averaged 0.4 cm (range 0.3 - 0.6 cm) in both the stomach and environment. Such small prey was never eaten by fish longer than 6.0 cm but, as demonstrated in laboratory experiments, small flounders are highly efficient in detecting and ingesting organisms of this length.

The maximum length of organism ingested by the fish measured 1.4 cm (Table 36), thus representing about 35% of the fork length. This value corresponds well with that of other comparably sized fish, a surprising feature considering the unusually small mouth dimensions of this species (Table 37). Direct observations in the laboratory, indicated, however, that flounders invariably "chew" large items in their mouth in order to reduce rigidness and thus facilitate ingestion.

The percentage of stomachs containing no identifiable remains fluctuated between 42 and 76% (Fig.79). Since the highest values occurred coincidently with the coolest water values, temperature may have been limiting feeding. The proportion of empty stomachs in large flounders (i.e. $>$ 6.0 cm) was always greater than that of the smaller individuals, perhaps reflecting metabolic rate. In addition, as previously mentioned, fish shorter than 6.0 cm catch prey more efficiently than large specimens.

The dry weight of stomach contents in specimens of 1 g averaged 19.7 mg during July, 13.3 mg in August and September, and 1.5 mg in October and November. These values are remarkably high compared with large flounders, a pattern again probably related to metabolic rate and hunting efficiency. The total weight of stomach contents, expressed in terms of body weight, was similar to that reported for a number of other temperate zone species of comparable size (Tyler, 1971). The fall in weight of ingested food during the study period can probably once again be attributed to fluctuations in water temperature.

Under experimental conditions in the laboratory, the flounders appeared to use visual stimuli to find prey, as has already been suggested is the case in other fish species (Healey, 1971). Observations in the laboratory showed that the fish normally moved across the bottom in short "hops" with pauses of variable length in between what is presumably their search for food. The exact moment of detection of prey was distinct, usually characterized by rapid movement, a quick alignment of the body with the organism and a dash with comparatively little of the "hopping" movement.

Large flounders ($>$ 6.0 cm) detected representatives of Asellus aquaticus measuring 1.0 cm in length at up to distances of 35 cm in clear water and 19 cm in turbid water (Fig. 80). The smallest organism seen in the clear tanks measured 0.24 cm while the corresponding value under turbid conditions averaged 0.30 cm. Thus, the absence of small ingested organisms in the reservoir catches can partly be attributed to visual limitations in turbid water. In addition, the high proportion of empty stomachs and the relatively small amount of ingested material is also possibly dependent on this factor. Small flounders could detect 1.0 cm representatives of Asellus as efficiently as individuals of greater length regardless of turbidity. However,

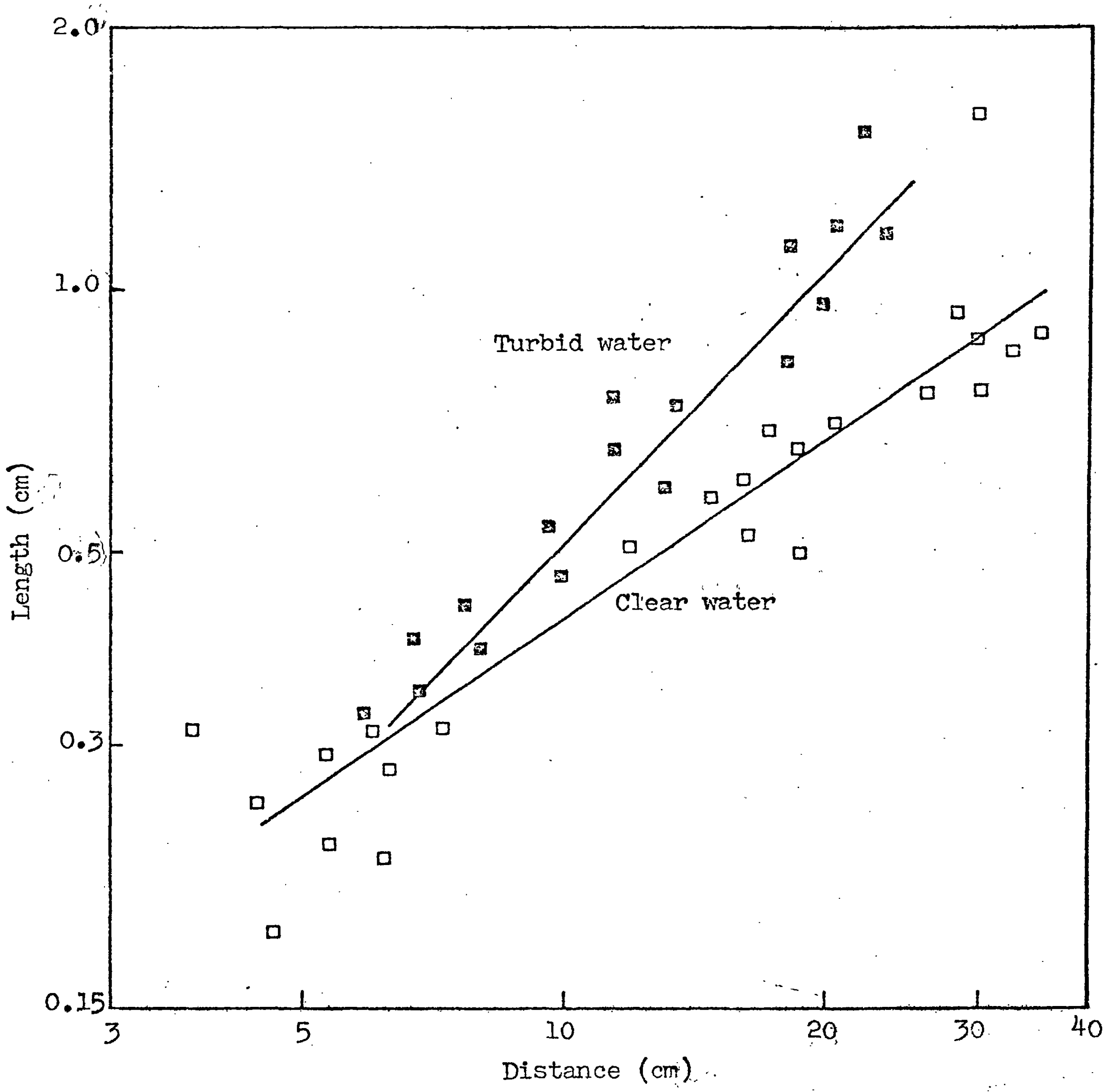

Fig. 80. The greatest distance representatives of <u>Asellus aquaticus</u> of different length were detected by flounders in clear (2-3 JTU) and turbid (85-90 JTU) water.

these small fish were better able to find small prey, individuals of 0.10 and 0.20 cm being detected in clear and turbid water respectively. This ability to catch the shorter organisms is reflected in the minimum length of stomach contents from the reservoir sample. In addition, as small flounders could detect prey over a relatively large area, it is not surprising that both the weight of stomach contents and the proportion of stomachs containing food remained high.

The time required for large flounders to catch representatives of Asellus 1.0 cm long in clear water varied from 0.9 sec at a distance of 3.0 cm to 2.9 sec at 20.0 cm with corresponding values under turbid conditions of 1.6 and 4.0 sec (Fig. 81). The fish apparently hesitated in chasing food in the latter experiments due to difficulties of recognition. Virtually identical patterns characterized flounders shorter than 6.0 cm.

The maximum distance fish of all size could see representatives of Gammarus pulex and the time required to swim to the prey was, regardless of water conditions, almost identical to that recorded for Asellus aquaticus. Fish were able, however, to catch prey in only 80% of the presentations (assuming 100% for Asellus) in turbid water reflecting the movement of the relatively motile Gammarus out of visual range before body alignment. A similar but more marked pattern was observed for the highly motile Eurydice pulchra. Thus, under turbid conditions, flounders of all size were able to catch this prey on only 3 - 4% of the times that it appeared within visual range and, in clear water, the corresponding value averaged 10%. The above data agree well with the scarcity of Eurydice in the fish collected from the reservoir. Large representatives of Crangon crangon (> 1.5 cm) were easily detected by flounders of both size classes. Almost invariably the fish swam as quickly as normal to the prey. However, at or near the moment of contact, Crangon tried to escape with two or three sharp movements, travelling at least 15 cm away from the fish in one sec. Under clear conditions, this species escaped from large individuals in approximately 55% of the encounters but in turbid water the corresponding value approached 100%. Small flounders, because of their slower swimming speed, seldom captured this prey under either clear or turbid conditions. These data thus

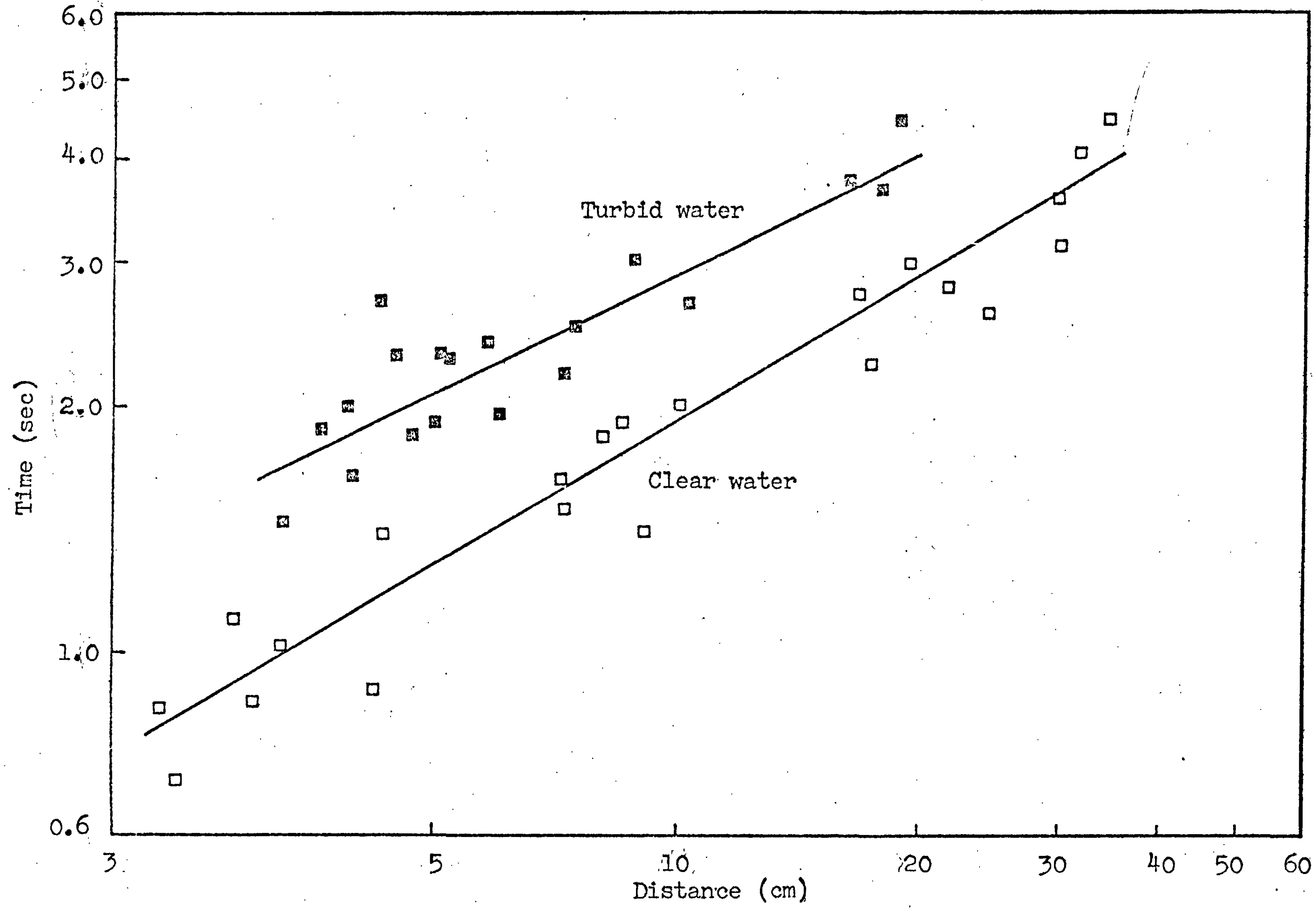

Fig.81 . The time required for flounders to capture representatives of *Asellus aquaticus* measuring 1.0 cm at different distances in clear (2-3 JTU) and turbid (85-90 JTU) water.

help at least partially to explain the relative scarcity of Crangon in the stomachs of fish collected from the estuary.

The greatest distance Macoma balthica was detected and the time used in swimming to it paralleled the data recorded for Asellus. However, the fish irrespective of size never swallowed this prey, which is surprising in view of the fact that flounders collected from the Bristol Channel approximately 100 km from the reservoir contained large amounts of this species in their stomachs. As molluscs occurred sparingly in the reservoir, but were exceedingly common at the other location, it appears that the fish had become conditioned to eating softer-bodied prey.

The ability of the flounders to catch the different prey species at relatively higher water temperatures, i.e. 20 and 25°C, was virtually identical to those described above. However, since at 8°C, the average temperature of the reservoir during the winter, the fish never chased either Crangon or Eurydice, these prey were seldom captured. In contrast, comparatively immotile organisms such as Asellus were captured with about the same efficiency as that exhibited at the higher water temperatures. Thus, during the winter months, both Crangon and Eurydice were seldom eaten by the estuarine fish, being largely replaced in the diet by the sedentary polychaete Nereis diversicolor.

Two of the most common prey species in the reservoir, Neomysis integer and Praunus flexuosus, proved unsuitable for experimentation. Direct field observations, however, indicated both organisms remained relatively immotile until disturbed. The subsequent escape reaction resembled that outlined for Crangon but, because of their smaller size, the distance travelled was comparatively short. Most fish in the reservoir should thus have little difficulty in catching these organisms.

The flounders were unable to detect any species of prey more than 15 cm above the substrate surface, either in clear or turbid water. Thus, organisms which occurred mainly near the surface of the reservoir, e.g. Eurydice pulchra, were rarely eaten. The fish saw representatives of Gammarus salinus as well as those of G. pulex, irrespective of turbidity. Thus colouring, at least in this case, had little to do with the efficiency of finding prey. Presumably movement of the organisms, which appeared identical, was the primary factor involved in detection.

Eels, Anguilla anguilla (L.)

Since very few eels contained food in their stomachs during the colder months, the data collected at this time are not included. The diet of non-migratory (yellow) eels, irrespective of size within the range 19.5 - 56.5 cm, consisted mainly of Crangon crangon and Neomysis integer, followed in much reduced numbers by Praunus flexuosus and Gammarus salinus. Crangon accounted for over 95% of the stomach contents in April but decreased uniformly in importance to only 20% in August when it was replaced with Neomysis integer. In September and October however, Crangon became more important (75%) and, in terms of dry weight, always accounted for at least 80% of the stomach contents. The relative importance of Crangon in the diet of eels is surprising considering that flounders, Platichthys flesus, captured from the reservoir seldom fed on this species, a pattern of selection based largely on the unusually quick escape reaction of Crangon. Direct observations in the laboratory, however, indicated that eels invariably approached prey slowly and did not exhibit the dash characteristic of flounders. Under these conditions, Crangon seldom attempted to escape and was thus easily captured. Neomysis, although frequently an important food item, was often ingested in disproportionately small quantities. Since its average length in the reservoir, 1.0 - 1.7 cm, approached the lower limit of commonly ingested prey (Table 36), selection against this species was based largely on size. Gammarus salinus and Eurydice pulchra were also rarely utilized even though they occurred abundantly in the reservoir, the basis of this selection probably being similar to that outlined for flounders. Fish (e.g. young flounders, gobies , sticklebacks etc.) were also never eaten, a surprising feature in view of the fact that they occurred abundantly towards the bottom and were of suitable size. Some studies (e.g. Godfrey, 1957; O'Conner, and Power, 1973) have reported that eels are highly piscivorous while others have suggested that they feed mainly on benthic invertebrates (Frost, 1946; Sinha and Jones, 1967a). This variation in diet indicates a preference for comparatively immotile prey (e.g. benthos) providing it occurs in sufficiently large numbers. This view agrees with the work of Burnet (1952) which suggested fish were a major prey because the invertebrate fauna was largely concealed among weeds.

The average length of Crangon crangon in the stomach during April and May was 5.3 cm (range 4.0 - 6.3 cm) implying little if any size selection existed at this time (Section 8). During June, however, the fish ingested only larger representatives of this organism (average length, 3.4 cm; range, 3.0 - 3.8 cm) even though organisms with a wide length range were available (Section 8). This selection for large individuals is particularly striking considering that much smaller representatives of Neomysis integer were frequently ingested. It therefore appears that the fish had become conditioned to larger representatives of Crangon during the early part of the study and thus continued to feed on these organisms during periods of low standing crop, a situation observed in other species (Ivlev, 1961). In addition, it is interesting to note that the eels must have been able to distinguish representatives of Crangon from those of Neomysis integer. During the remainder of the study, the average length of Crangon crangon in the stomachs was generally similar to that in the environment. Similarly, the length of ingested Neomysis invariably paralleled that in the reservoir with , for example, the April and August values averaging 1.72 and 1.13 cm respectively, compared with 1.74 and 1.01 cm in the estuary.

The average length of ingested organism did not increase with the size of fish. During April , for example, representatives of Crangon crangon ingested by eels 30 - 35 cm in length averaged 4.9 cm while those longer than 55 cm contained specimens of approximately 4.7 cm .

The maximum length of frequently ingested organism increased from 3.0 cm in fish of 15.0 - 25.0 cm to 6.5 cm in specimens measuring 45.1 - 55.0 cm (Table 36). These values correspond to approximately 15 and 13% respectively of the fork length and are thus much lower than those reported for other fish predators (Popova, 1967; Reshetnikov et al., 1972; Moore and Moore, 1974) and reflect the eel's disproportionately long body. Expressing the mouth dimensions of this species as a percentage of fork length gives values of approximately 2.6% for the width and 2.1% for the height (Table 37), proportions considerably lower than those recorded for other fishes in this study and again reflecting the animal's shape. In absolute terms, the mouth of eels 35.1 - 45.0 cm in length measured approximately 1.0 cm (width) by 0.9 cm (height) giving a frontal area of roughly 0.9 cm^2. Expressing the maximum length of ingested organism as a proportion of this latter figure gives a value of 5.4. The corresponding data for whiting (Merlangius merlangus (L.)) measuring 10.1 - 15.0 cm in length, for example, are 0.9 cm^2 and 4.2 respectively. Thus, an eel whose mouth was 1.0 cm^2 in area could have ingested organisms up to 5.4 cm in length while the corresponding value for whiting was 4.2 cm. These data imply that eels have no unusual restrictions imposed on their feeding even though analyses using fork length may indicate the opposite pattern. Crangon crangon had the greatest girth of all prey species measuring 6.0 and 9.0 mm in diameter for specimens of 3.0 and 6.5 cm respectively. Since these values are less than the smallest dimensions of the mouth of eels in the size classes 15.0 - 25.0 and 45.1 - 55.0 cm, the exclusion of this species from the stomach contents is not due to the girth of the prey.

The percentage of stomachs containing no identifiable remains was unusually high, averaging over 90% during the winter but falling to 30% in August and 50% in September (Fig. 82). These values agree well with those given by Sinha and Jones (1967a) and the data of Markowski (1966) also indicate a high proportion of empty stomachs. Seasonal changes in the feeding intensity of eels are apparently dependent on temperature, Sinha and Jones (1967a,b), for example, suggesting that little if any food is consumed below 10 - 12°C. In the present study the reservoir water remained below 10°C between January and May and again towards the end of the investigation, coincident with the greatest numbers of non-feeding animals. During the warmer months, changes in the standing crop of prey seemed to bear little correlation with the proportion of feeding animals. For example, more fish were found with food in their stomachs during August than at any other time but the amount of available prey approached the lowest levels recorded during the study. Presumably

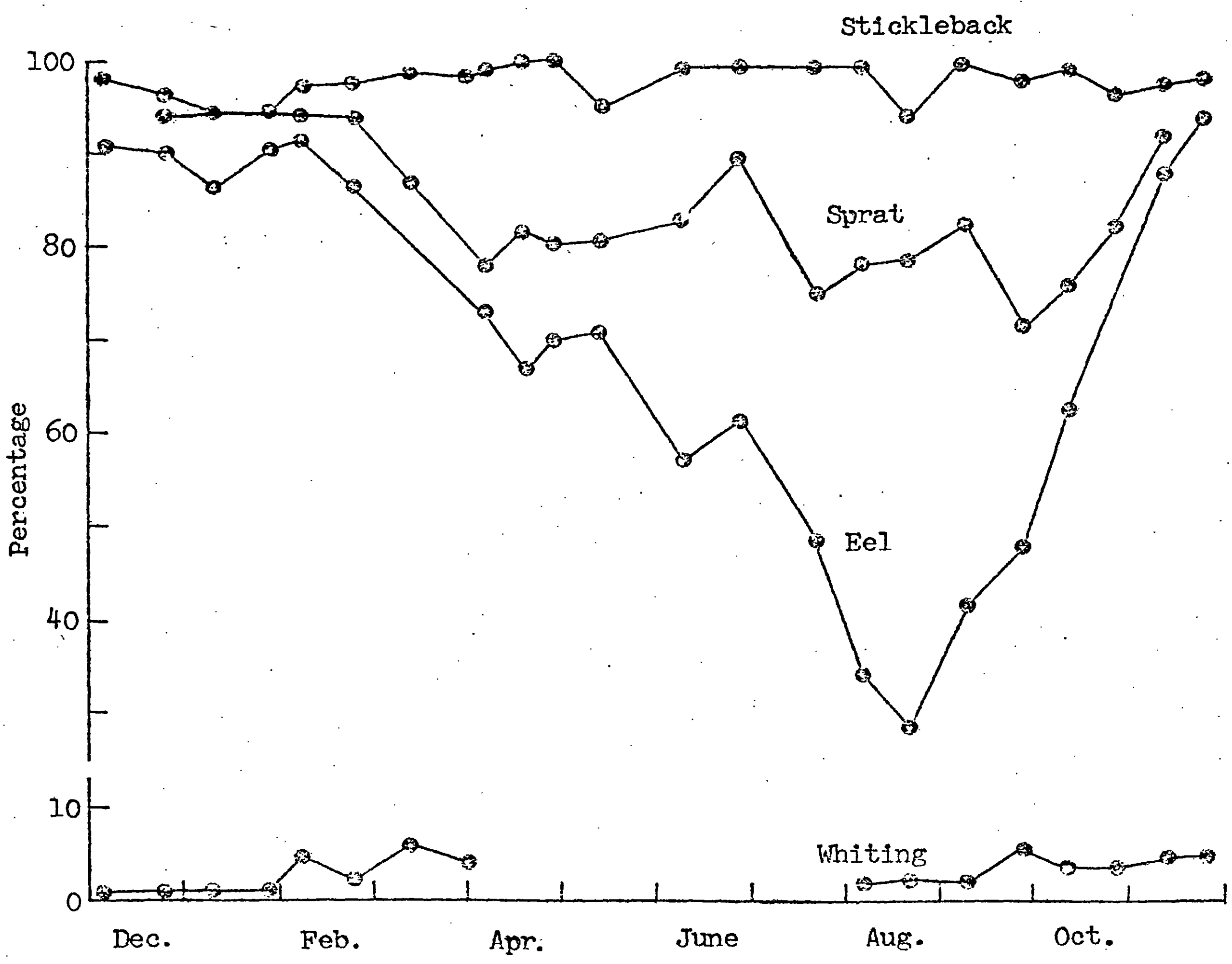

Fig.82 . Percentage of stomachs that contained no identifiable remains in some fishes collected from the Severn Estuary.

fluctuations in the generally high level of turbidity in the estuary had significantly influenced changes in the proportion of feeding animals during the warmer months of the study. The percentage of stomachs which contained no identifiable remains, although apparently typical of eels, was high in relation to many other fishes (Lawler, 1965; Tyler, 1971). As the rate of gastric evacuation of eels is similar to that of most other species in the northern temperate zone (Burnet, 1952; Sinha and Jones, 1967a), it appears that this high percentage reflects a generally low level of feeding activity regardless of environmental conditions.

The dry weight of stomach contents fluctuated a great deal throughout the study (Table 38). During the colder months, for example, few fish contained any food in their stomachs but during April and May approximately 142 mg of ingested material was found in specimens of 50 g while between June and September the corresponding figure averaged 98.6 mg. Similarly, the mean values for 100 g specimens during these latter two periods were 736 and 177 mg respectively. The scarcity of ingested material during the winter undoubtedly reflects the influence of cold water and temperatures on feeding activity and metabolic rate. The unusually high values recorded in April and May when temperatures averaged 10°C probably resulted from the fact that the rate of feeding was faster than that of digestion. The weight of stomach contents during the warmer months was comparable to several other species (Tyler, 1971; Moore and Moore, 1974).

No food was found in the stomachs of migratory (silver) eels which measured from 41.2 to 79.3 cm in length. In contrast, Frost (1946) reported that a considerable portion of animals caught in freshwater were actively feeding while Wheeler (1969) indicated that specimens captured at sea usually contained no food.

Elvers, measuring from 5.5 to 8.1 cm in length and captured during the spring,always had food in their stomachs. The ingested material usually consisted of detritus but a few fish contained fragments of macrophytic green algae and in no instance were the remains of animals distinguishable. The general absence of algae from the stomachs reflects their scarcity in the environment. Similarly, few if any animals were eaten because of the almost total absence in the reservoir of small organisms such as copepods. As the stomach contents of the elvers usually contained an amorphous mixture of detritus, estimates of the size of ingested particle could not be obtained. Furthermore, no data concerning the weight of stomach contents were collected since, in dissecting out the gut, ingested material moved from the stomach into the intestine and vice versa.

Whiting, Merlangius merlangus(L.)

Since only a few whiting were captured between April and July, the limited data from this time do not warrant description. Throughout the investigation, the diet of fish measuring 2.8 - 15.0 cm in length usually consisted of Neomysis integer, followed in much reduced numbers by Crangon crangon, Gammarus salinus, Praunus flexuosus and Pomatoschistus minutus, a point exemplified by the August data (Fig. 83). The predominance of Neomysis in the stomachs is surprising in view of its relative scarcity in the reservoir for much of the sampling period. However, both Gammarus salinus and Eurydice pulchra also often occurred in relatively small numbers in the intake samples and their accessibility was often highly restricted. Furthermore, although Crangon crangon sometimes occurred in large quantities in the reservoir, the length of this species usually exceeded the maximum size of ingested organism, i.e. 1.4 - 5.4 cm. Since Praunus flexuosus was also comparatively large, a similar pattern may be attributed to this species. It therefore appears that the abundance of Neomysis in the stomachs reflects the scarcity of other suitable prey in the environment and is not related to preference for this species.

As previously mentioned, part of the reason why Eurydice pulchra was not eaten in large numbers by the whiting is due to its spatial distribution in the water column during part of the tidal cycle. During periods of low tide, however, it must have occurred in the same habitat as the whitings, indicating selection against this species. The scarcity of Eurydice in the stomachs of fish longer than 5.0 cm could possibly be attributed to size selection since its average length in the environment, 0.3 - 0.4 cm, was either similar to or less than the smallest organism ingested (Table 36). Whiting shorter than 5.0 cm also did not consume Eurydice as frequently as it occurred in the environment despite the fact that the size of these potential

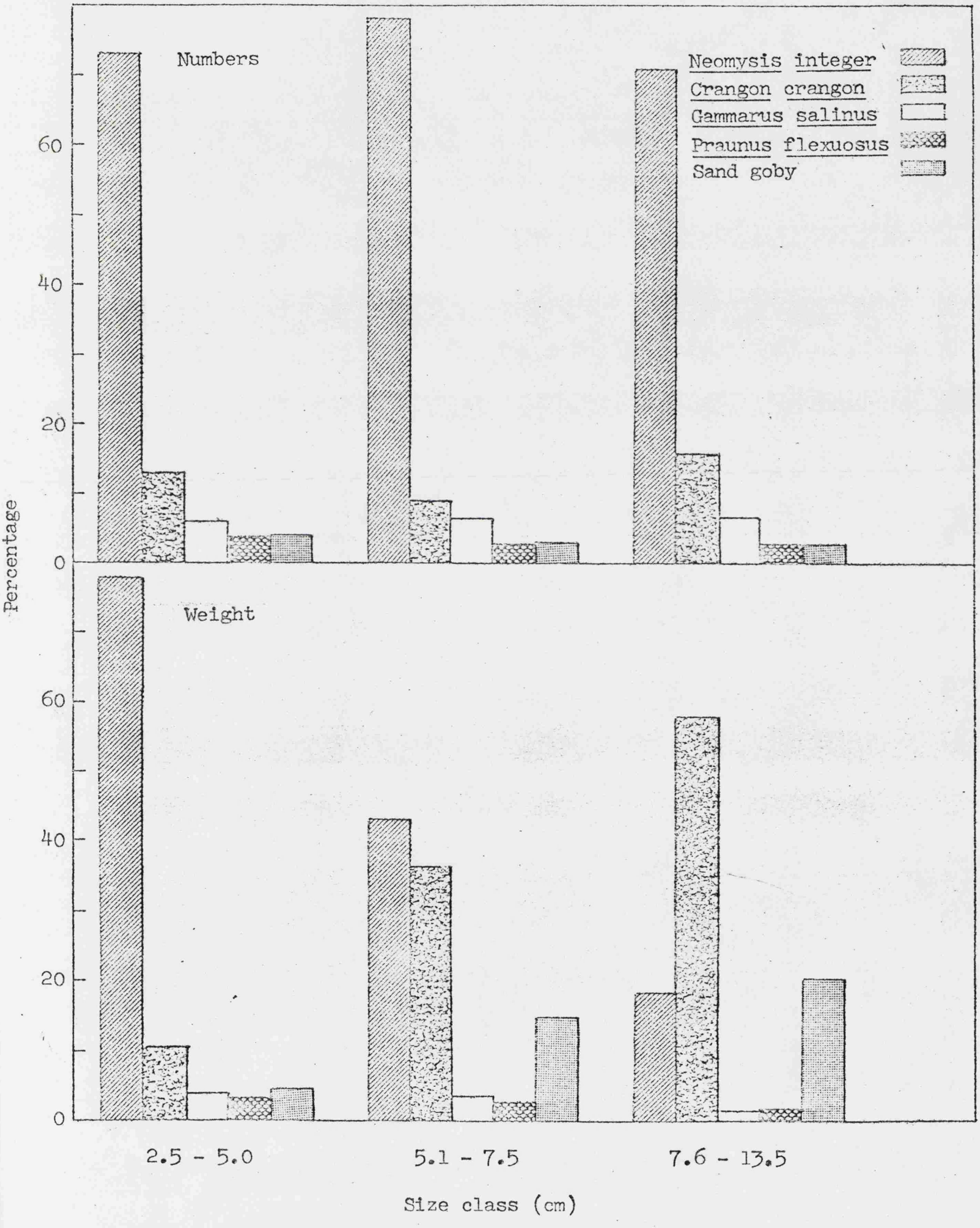

Fig. 83 . Composition of stomach contents, expressed as a percentage in terms of numbers and dry weight, of whiting of different size collected from the Severn Estuary during August, 1974.

prey lies within the length range of organisms often ingested by these smaller individuals. In an attempt to explain this scarcity of ingested Eurydice, a number of whiting were brought into the laboratory for experimental feeding studies but unfortunately it was not possible to maintain them for more than a few hours. Since laboratory studies on flounder indicated that the unusually quick movements of Eurydice result in an insufficiently brief contact time with the fish for detection and capture, it seems possible that a similar situation might exist with respect to whitings.

A considerable shift in the species composition of the diet with the size of fish was occasionally observed. During September, for example, Neomysis was the most abundant organism (60% by numbers) found among the stomach contents of whiting shorter than 5.0 cm, followed by C. crangon (28%) and G. salinus (8%) (Fig. 84). Larger fish, however, ate comparatively few of the former species (24 - 36%) with the numbers of C. crangon in the stomachs contributing a greater amount (52 - 66.5%). This change in the regular pattern of feeding is undoubtedly due to the simultaneous rise in the reservoir in the abundance of small Crangon which are easily consumed by large fish but too long for smaller individuals.

In terms of dry weight, Neomysis was by far the most common organism in the stomachs of whiting shorter than 5.0 cm during much of the study, followed in order of descending importance by Crangon crangon, Pomatoschistus minutus, Gammarus salinus and Praunus flexuosus (Fig. 83). Within the size class 5.1 - 7.5 cm, however, Neomysis was always of less importance, contributing for example, about 43% of the stomach contents during August, (Fig. 83), with a corresponding increase in the amount of C. crangon (36.5%) and P. minutus (15%). This pattern was even more exaggerated in fish longer than 7.6 cm with Neomysis falling to only 18.5% and with C. crangon and P. minutus rising to 58 and 20.5% respectively. As illustrated in Figs 78 and 85 these changes in diet with size are apparently not related to fluctuations in numbers but are due rather to the fact that the average size of both C. crangon and P. minutus increased with the length of whiting while that of Gammarus and Neomysis remained relatively constant (Fig. 85). During September, when there was a sharp rise in the availability and utilization of Crangon (Fig. 84), Neomysis integer was of

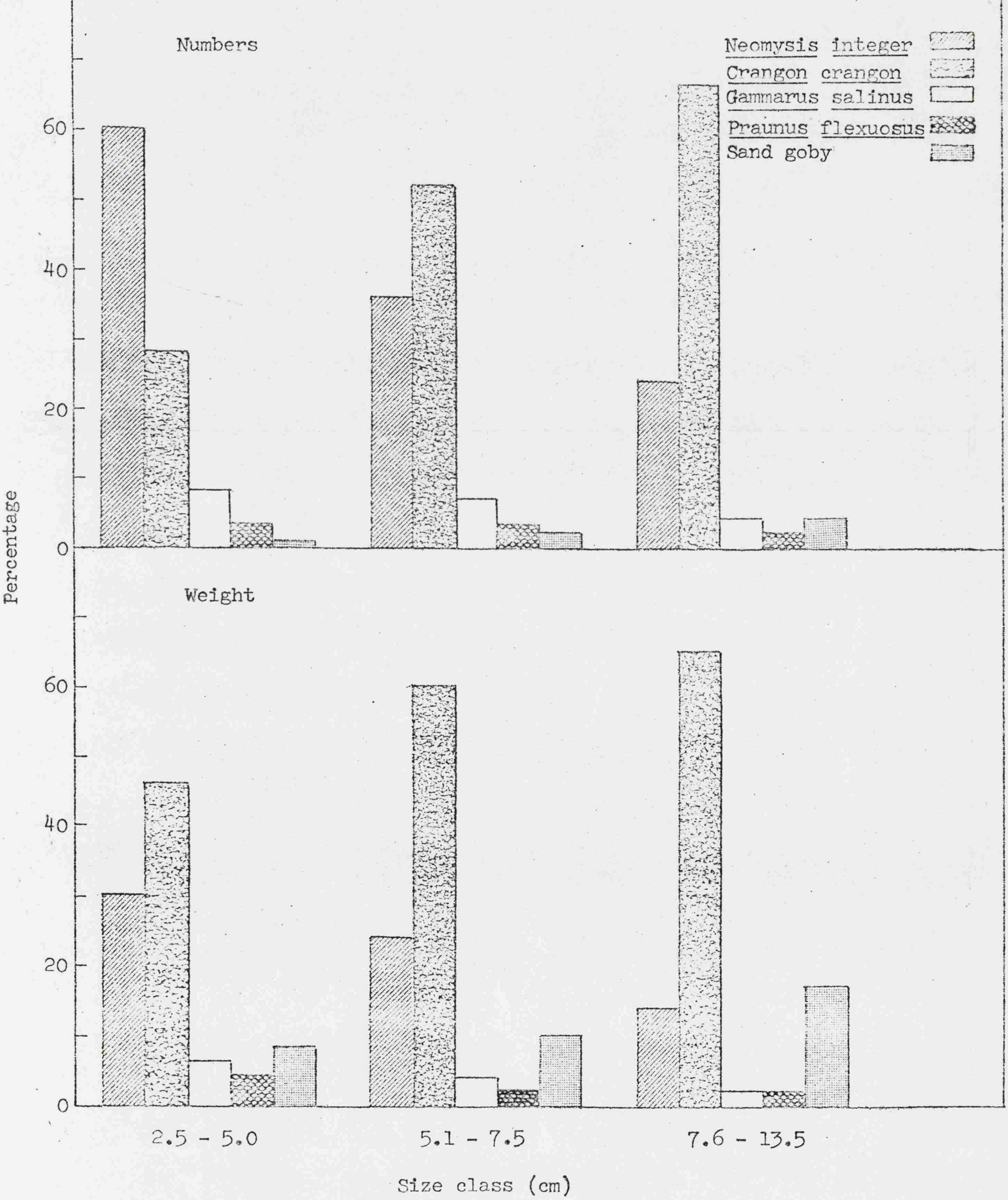

Fig. 84 . Composition of stomach contents, expressed as a percentage in terms of numbers and dry weight, of whiting of different size collected from the Severn Estuary during September, 1974.

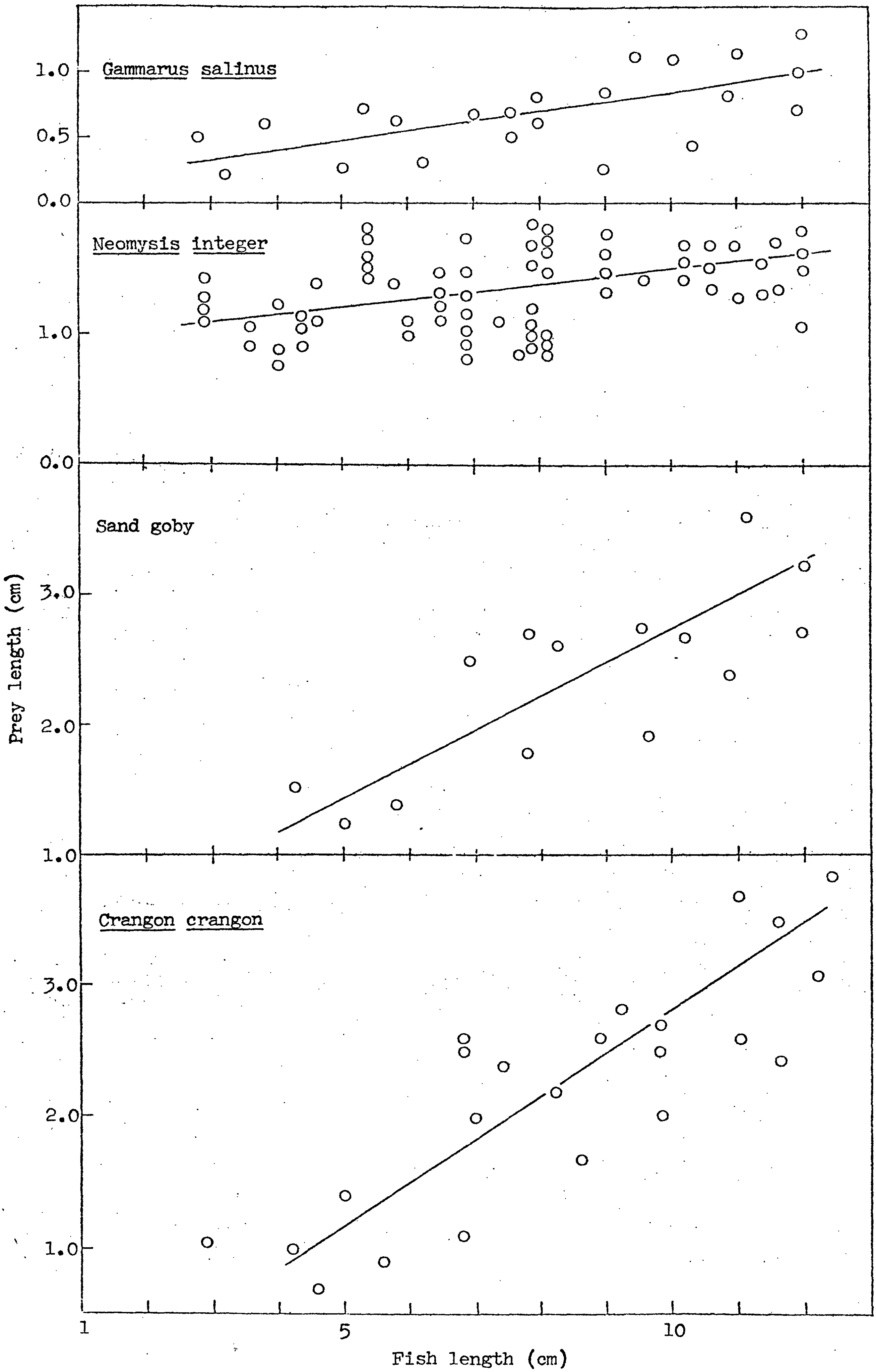

Fig. 85. Changes in the size of prey with the length of whiting collected from the Severn Estuary during August, 1974. Each point represents an individual

comparatively little importance.

Nagabhushanam (1965) reported that small whiting often feed heavily on copepods and other relatively small prey such as decapod larvae. These organisms were never ingested by the fish captured from the Severn Estuary, reflecting their scarcity and perhaps even their absence from the environment. Larger fish in Nagabhushanam's study fed heavily on mysid and amphipod species comparable to those in the present study. Similarly, large fish ingested Crangon more frequently than small fish, a pattern of selection explained for the Severn stocks. Polychaetes were heavily utilized in Nagabhushanam's study but were never eaten in the reservoir. Presumably, the utilization of the buried fauna was limited by the great abundance of non-burrowing prey.

The average length of the most commonly ingested species increased with the size of fish (Fig. 86). During August, for example, representatives of Crangon crangon had an average length of about 1.0 cm in fish of 4.0 cm rising to 2.7 cm in animals measuring 10.0 cm. Expressing the above data as a percentage of fork length indicated that the size of ingested prey increased with the size of whiting on a unit length basis, a surprising feature considering that the relative mouth dimensions had fallen (Table 37). This indicates that the size of the buccal and/or pharyngeal cavities and/or the stomach had restricted prey size in the smaller fish rather than the dimensions of the mouth. The length of ingested representatives of Pomatoschistus minutus also increased sharply with the fish size, rising from about 1.2 cm in fish measuring 4.0 cm to 2.75 cm in specimens of 10.0 cm. In contrast, however, other organisms such as Neomysis and Gammarus, showed only a slight increase in size with fish length. The increase in the length of prey with fish size, noted for some species in this and other studies (e.g. Chilvers and Gee, 1974; Lewis, 1974) was observed neither in eels nor in flounders collected from the reservoir. These data suggest that this pattern of size selection, at least in certain instances, is species dependent. For those fish which consume increasingly larger objects as they grow, the effect of predation is spread more evenly among the different stages of the prey's life cycle.

The maximum length of ingested organism increased from about 1.6 cm in whiting measuring less than 5.0 cm to 3.9 cm for those longer than 12.5 cm (Table 36). These values represent about 40 and 38% respectively of the fork length and are thus remarkably similar considering the much sharper decrease in relative mouth dimensions (Table 37). The value obtained for the large fish was similar to that reported for several other species of comparable size but the corresponding value for fish shorter than 5.0 cm was relatively small. As previously mentioned, the maximum length of ingested organism, expressed as a proportion of the frontal area of the mouth in fish longer than 10.0 cm , was 4.2 while the corresponding figure in whiting measuring less than 5.0 cm in length was about 93.0 . These data imply that large fish with a mouth area of 1.0 cm^2 could ingest organisms up to 4.2 cm in length while smaller fish could, on a unit basis, ingest prey of 93 cm. Thus, the small whiting consumed disproportionately large objects even though such a pattern was only poorly illustrated when expressed as a percentage of fork length. Nagabhushanam (1965) reported that the maximum length of organism ingested by whiting measuring up to 45.0 cm in length was approximately 10 cm, thus representing about 20% of the fish's length. As with eels, the diameter of the largest prey organism was always less than the smallest dimension of the fish's mouth.

The length of the smallest organism ingested by the whiting, 0.2 - 0.25 cm , was the same regardless of the size of fish (Table 36). That this value is much smaller than that obtained for eels presumably reflects the relative hunting efficiency of the two species. In many fish the minimum length of ingested prey increases with the size of the individual (e.g. Moore and Moore, 1974) but in other instances the values remain relatively constant (Popova, 1965), indicating that the change in hunting efficiency with age is species dependent. Copepods are often ingested by whiting in other areas (e.g. Nagabhushanam, 1965) and thus the minimum length of ingested organism is smaller than that found in this study, reflecting the difficulty of seeing small organisms in the turbid waters of the reservoir.

Virtually all the whiting invariably contained food in their stomachs (Fig. 82). Turbidity, the major factor influencing feeding of many fishes in the estuary, apparently had an insignificant influence on the whiting, suggesting this species is a comparatively active hunter. The dry weight of material found in the stomachs of whiting remained constant during the study averaging 1.28 and 41.7 mg for fish of 1.0 and 5.0 g respectively (Table 38). The consistency of values over the study period indicates that changes in the number of prey in the environment and water temperatures had little influence on feeding. Since whiting had considerably more food in their stomachs on a unit weight basis than eels, together with the fact that a higher percentage of their stomachs contained food, it appears that whiting could have had a greater effect on the numbers of prey than eels.

The foregoing feeding studies were based on fish collected at or near high tide during the day. Since the weight of stomach contents of specimens captured at low tide was usually similar to that outlined above, it appears that feeding occurs at about the same intensity irrespective of tidal conditions. In the context of feeding periodicities, it is worth noting that Nagabhushanam (1965) suggested that whiting follow swarms of amphipods, isopods and mysids into the intertidal zone at night to feed, which may imply that insufficient numbers of prey occurred elsewhere. This pattern was not observed in the present study but in both instances feeding occurred when the standing crop of prey was relatively high.

The species and size composition of the food of bib (_Trisopterus luscus_ (L.)) and poor cod (_T. minutus_ (L.)) were virtually identical to those described for whiting. The dry weight of food in the stomachs of bib averaged, however, considerably less than that of whiting, e.g. individuals of 1.0 and 5.0 g contained about 0.8 and 30.5 mg of ingested material (Table 38). The weight of stomach contents of 1.0 g poor cod, 1.3 mg, was similar to that of whiting of comparable size whereas cod weighing 5.0 g contained only about 32.9 mg of food in their stomachs.

Sprat, Sprattus sprattus (L.)

Since only a few sprats were captured during the colder months, the data obtained during this time will not be described. Between April and June sprats measuring from 4.5 to 15.6 cm in length fed almost exclusively (greater than 80% by numbers) on Gammarus salinus. Thereafter, this species was replaced almost entirely by Neomysis integer except towards the end of September and most of October when Crangon crangon also became important (20%). The great abundance of Gammarus in the stomachs during the early part of the study is undoubtedly due to the fact that other potential prey species, mainly because of their long length, were unsuitable for consumption. For example, the largest organism, 1.5 cm, found in the stomach, was always smaller than the average size of available representatives of Crangon crangon and Praunus flexuosus. Similarly, the average length of Neomysis integer exceeded 1.5 cm in April and thereafter remained at relatively high levels. Representatives of Gammarus salinus in the intake samples, on the other hand, averaged 0.6 - 0.8 cm in length and always occurred in considerable numbers (38 - 75% of the total invertebrate fauna). The increase in the relative abundance of ingested Neomysis in June corresponds well with a simultaneous rise in numbers in the environment. Since the average length of this species in the reservoir decreased to under 1.2 cm, the effect of size limitations was greatly reduced. Crangon crangon achieved considerable importance in the stomachs during the latter part of the study. Since, as previously mentioned, large quantities of young appeared in the reservoir at this time, their abundance in the fish is undoubtedly related to the availability of suitably sized and relatively immotile organisms. Eurydice pulchra, although small (less than 0.5 cm) and occurring abundantly in the environment, was rarely consumed, a pattern observed for other fishes in the estuary. Presumably, the unusually high level of motility exhibited by Eurydice was an important factor in selection, a view supported by the fact that the food of the young sprats and other clupeids such as herring in many areas often consists of relatively immotile copepods (Ogilvie, 1934; Savage, 1931, 1937; Marshall et al., 1939) and planktonic gastropods and invertebrate eggs (Lebour, 1921a,b). Many other fishes in the estuary rarely ate Eurydice because of its unusual spatial distribution.

As the area was often exceptionally turbid, however, the sprats would possibly feed towards the surface (Battle _et al_., 1936) and thus this factor would be of little importance in selection. The diet of the Severn Estuary fish differed considerably from most other populations around the British Isles (e.g. Hardy, 1924), a feature undoubtedly related to the scarcity and perhaps absence of copepods from the environment during the sprat's period of residence. Marshall _et al_., (1939) have pointed out that young herring may migrate offshore daily to feed and thus little correlation existed between their inshore plankton samples and stomach contents. The fact that this pattern was not observed in the present study can probably be attributed to the influence of the reservoir on fish behaviour.

Monthly changes in the relative importance of the different food species in terms of dry weight almost exactly paralleled those outlined for numbers. However, during the latter part of the study, _Crangon crangon_ assumed disproportionate significance (35%).

Since the average length of _Gammarus salinus_ in the stomachs of the sprats was always less than 0.4 cm , a considerable degree of size selection is apparently operating. Similarly, the length of ingested representatives of _Neomysis integer_ never averaged more than 0.9 cm even though the mean values from the reservoir ranged from 0.9 to 1.8 cm. The average length of _Crangon crangon_ in the stomachs was also considerably less than that in the environment. This general selection for short prey is undoubtedly related, at least in part, to the fish's small size and its comparatively small mouth dimensions (Table 37). In addition, the mouth of sprats appears to be much more delicate than that of the other species investigated in this study and thus the struggling of larger prey could possibly cause structural damage. This latter point is presumably one of the reasons why copepods and other relatively immotile prey are often the most important dietary items in young herring and sprat. The average length of ingested organism, regardless of species, was usually less than that consumed by eels, gadoids and flounders, suggesting that little competition existed for the food of the sprats.

Although most fishes in the estuary probably have considerable difficulty in seeing small prey because of the turbid conditions, the degree of influence of this factor on feeding is still apparently species dependent. As sprats and herrings usually consume much smaller prey (e.g. copepods) than most other estuarine fishes, it seems likely that they would have correspondingly less difficulty in detecting prey in turbid water. Unfortunately, this latter hypothesis could not be tested in the laboratory because the sprats collected from the reservoir invariably died within a few hours of being brought back to the laboratory.

The maximum length of ingested organism increased from 1.2 cm in fish measuring less than 5.0 cm to 1.5 cm for those between 7.6 and 10.0 cm (Table 36). These values represent only about 27 and 22% respectively of the fork length and may reflect the difficulty involved in catching large organisms with its rather delicate mouth. In addition, relatively large representatives of Crangon, Praunus and Neomysis exhibit a marked escape reaction which sprats, presumably adapted to feed most efficiently on immotile prey (e.g. copepods), could probably not compensate for. These views are supported by the fact that the maximum length of ingested organism, expressed as a proportion of the mouth area, never exceeded 15 compared with, for example, a value of 93 in young whiting. The minimum length of ingested prey, 0.1 - 0.2 cm (Table 36), was smaller than that consumed by any other species of fish in the study and was similar to that recorded for the smallest organism found in the reservoir, reflecting the previously mentioned ability of sprats to catch unusually short prey.

The percentage of stomachs containing no identifiable remains averaged about 85% and never fell below 70% (Fig. 82), values which are high compared with those given for other sprat and herring populations (Brook and Calderwood, 1885; De Silva, 1973), a feature undoubtedly related to the general scarcity of small prey. As several authors (e.g. Hardy, 1924, 1959; Andriyashev, 1964) have indicated that the greatest feeding intensity in clupeids occurs during the summer, it is unlikely that the high water temperatures had restricted feeding in the present study. As relatively few sprats contained food in their stomachs, the following estimates of dry weight are based on only 10 - 15 samples per month. The dry weight of the stomach contents appeared to be similar throughout the study averaging about 0.5 and 1.0 mg in fish of 1.0 and 5.0 g respectively. These values are much lower than those recorded for other species both in this study and elsewhere, suggesting that sprats, at least in this part of the estuary, are highly limited in their feeding activities. Presumably, the basis of this pattern is similar to that described earlier concerning the high precentage of empty stomachs. Hardy (1959) reported that young sprats and herrings in the Thames Estuary fed actively throughout the summer.

Several samples of sprats were collected at low tide but the proportion of empty stomachs remained unusually high (80 - 85%) and the dry weight of food in the stomachs appeared similar to the values recorded at high tide. Thus, tidal state apparently has little influence on feeding under the estuarine conditions of the present study at least. Marshall et al. (1939) reported that young herring feed throughout the day and night but the greatest intensity usually occurrs at dusk, apparently irrespective of tidal state.

Three-Spined Stickleback, Gasterosteus aculeatus L.

Large numbers of sticklebacks measuring from 4.0 to 6.5 cm in length were captured throughout the study but, in almost all instances, their stomachs were empty (Fig. 82). These data are particularly striking considering another population living under much the same conditions as those of the present study, contained large amounts of ingested food (Markowski, 1966). The high proportion of empty stomachs is certainly not related to availability of prey in the reservoir as a wide range of organisms was always present. Similarly, water temperatures and salinity could not have significantly affected the normal feeding behaviour of the species (Wheeler, 1969) and there was no indication that the fish in this part of the estuary fed mainly during the hours of darkness as specimens captured towards dusk and in the early morning also had empty stomachs. In an attempt to elucidate the cause of the feeding restriction, a number of sticklebacks, collected from the reservoir during May, were brought back to the laboratory and maintained in 140 l glass aquaria at 15°C. After an acclimation period of 30 days, the greatest distance the fish could detect two different prey species and the time required to catch these organisms was estimated in both clear (2 - 3 JTU) and turbid (85 - 90 JTU) water. In the clear water, representatives of the isopod Asellus aquaticus L. and the amphipod Gammarus pulex L. measuring 1.0 cm in length were detected up to a maximum distance of 44 cm while the corresponding value under turbid conditions was 26 cm (Fig. 86). The time required to capture animals of similar length at a distance of 10 cm averaged 1.1 and 1.5 sec respectively (Fig. 87). Although these data indicate that sticklebacks are much more efficient hunters than flounders, representatives of the latter caught in the estuary generally contained much larger amounts of food in their stomachs. A combination of several factors in the reservoir may therefore have produced environmental conditions less suitable for feeding in the sticklebacks.

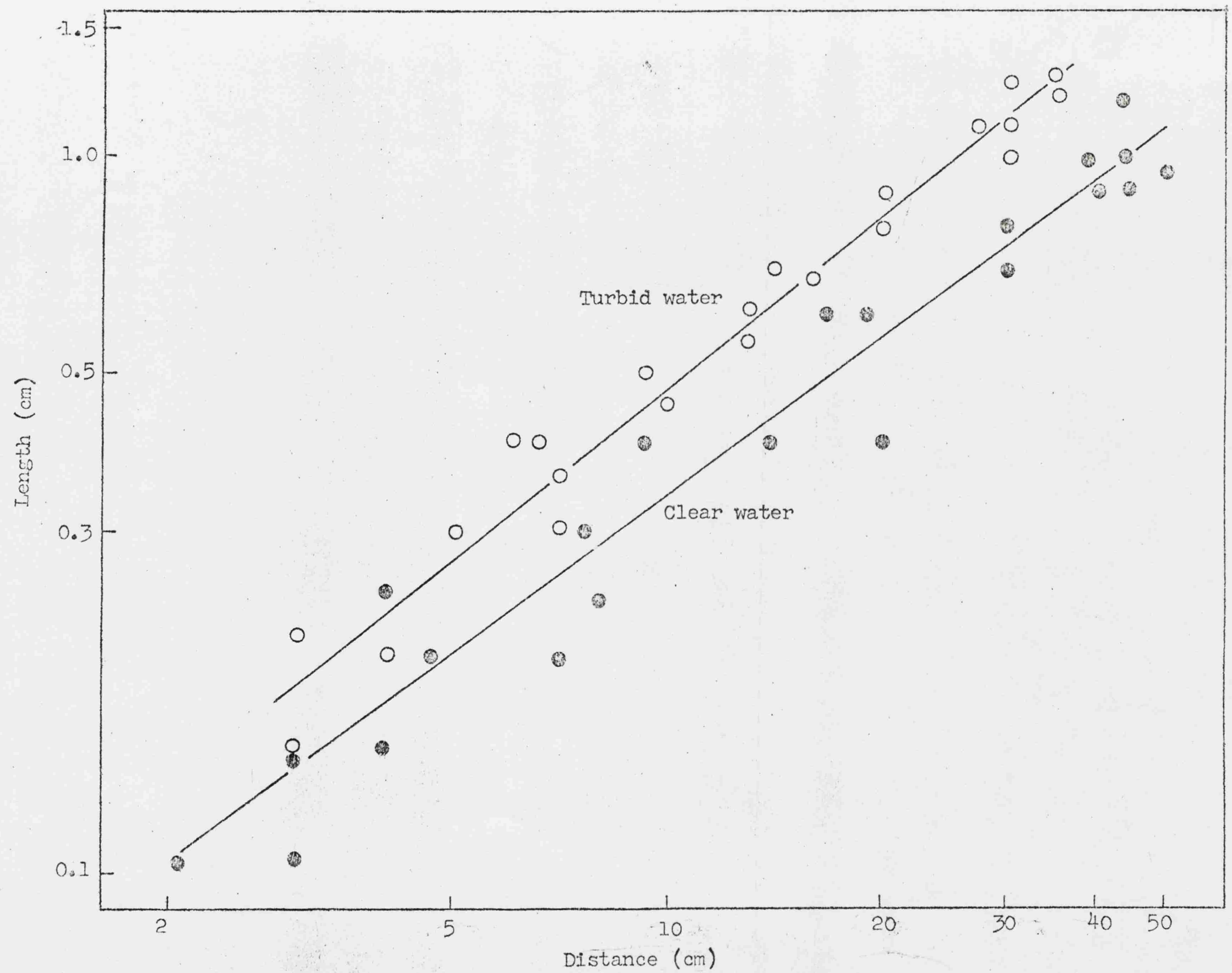

Fig.86. The greatest distance representatives of *Asellus aquaticus* of different length were detected by sticklebacks in clear (2-3 JTU) and turbid (85-90 JTU) water.

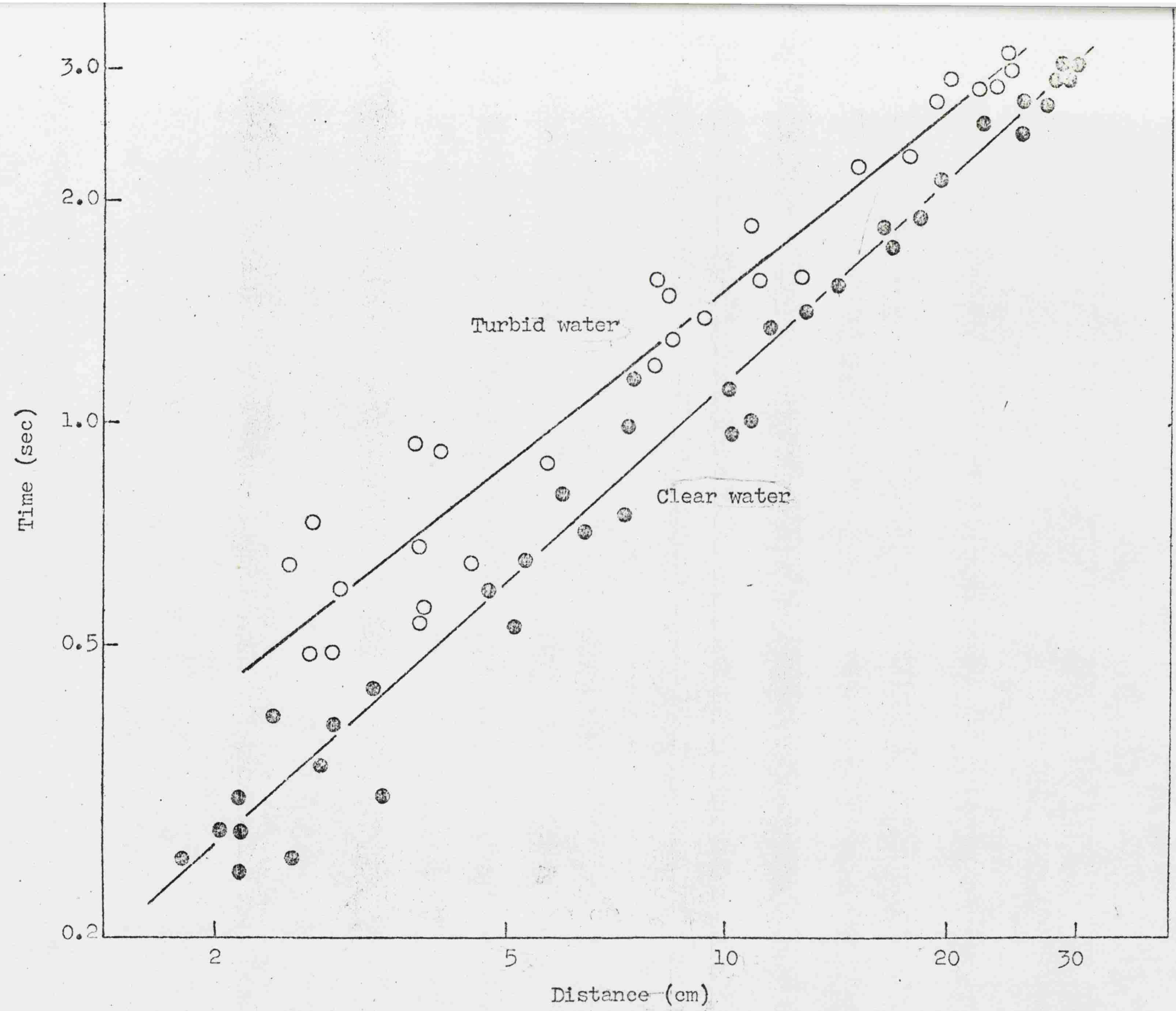

Fig.87 . The time required for sticklebacks to capture representatives of <u>Asellus aquaticus</u> measuring 1.0 cm at different distances in clear (2-3 JTU) and turbid (85-90 JTU) water.

10. Conclusions and Discussion

The studies on the ecology of the microflora in running waters show that the amount of algae available to herbivores varies considerably at different times. While most of the various algal communities exhibit a pronounced spring bloom, a feature apparently associated with increasing day length, the subsequent pattern of development is often highly variable and dependent on environmental conditions. In many cases, the effects of flooding are of particular importance. Thus, whereas initially they can bring about a reduction in the total standing crop, they are also apparently essential for the "renovation" of some substrates, such as those comprising the sediments. Thus, large amounts of epipelic algae were found in the summer and early autumn only during 1973 when flooding occurred in the period after the large spring bloom.

In terms of a food source, it was of relevance that algae from field collections showed no consistent and marked seasonal variation in the amount of lipid. Thus, the increased lipid deposition and growth of microphagous feeders during the spring and summer is presumably due to an elevation in the amount of algae and to the increased metabolism of the animal, rather than to a change in the composition of the flora.

One consistent feature found in *Asellus*, *Gammarus* and larval lampreys, all of which utilize algae as a food source, is the effect of temperature on digestion. Thus, while at both low and high temperatures a number of algal cells pass through sufficiently unharmed to be cultured successfully, the incidence of live cells in the hind end of the gut is much greater under winter conditions. Paralleling Prus' (1971) findings for *Asellus*, the assimilation efficiency of another herbivore, namely the larval lamprey, is relatively low and highly variable. The variability at a given temperature may be due to variations in the length of time the food remains in the gut, a feature which in turn may be correlated with the amount of movement the animal is exhibiting. While the actual volume of algae in the gut of *Asellus* and *Gammarus* is usually less than 50% of the total gut contents, this almost certainly does not represent its relative nutritive value. For example, the total amount of protein, lipid and carbohydrate (excluding cellulose) generally represented at least 80% of the total dry weight of unicellular green algae, whereas these components only made up 30% in the detritus fraction. In the context of detritus and algae in the suspended and epilithic material in the environment, it was perhaps surprising to find that the microflora only contributed a relatively small amount to the total organic component.

Some evidence was found that the greater productivity of the River Chew compared with Highland Water may account for the brook lampreys from the former area having a higher Condition Factor and attaining a larger size at metamorphosis. This is despite the fact that even in the Chew the volume of algae in the gut represented a maximum of 1.5% of the total contents. Only in the case of Paramecium in Wellow Brook was any evidence found for a herbivore having a marked effect on the microflora.

While emphasis has so far been placed on the role of algae in the nutrition of herbivores, the laboratory studies on larval lampreys clearly demonstrated that at 15°C these animals could also grow on detritus collected from a natural environment. Bacteria, on the other hand, were insufficient at all but the highest concentrations for promoting increases in weight.

While this study has attempted to quantify some aspects relating to the role of algae, detritus and bacteria in the diet of selected herbivores, much of the information we have at present should be treated with a certain amount of caution. For example, the relative composition of these components in the gut can be misleading and it is clearly essential that other factors, such as their potential nutritive value and digestibility must be further investigated. In addition, there is little doubt that the methods for assessing the relative volume of algae in the gut developed during the present study almost certainly yield rather conservative values.

In the study of the various algal assemblages, some important features became apparent in addition to those already mentioned. For example, in the case of epiphytes, particularly those attached to water cress and pond weed, the lack of attachment sites frequently limited development during the summer. Although the amount of suspended debris which had settled on the host plant never affected the standing crop of the associated microflora, a high rate of water flow caused an increase in the detachment rate of the epiphytes and may also have limited the rate of cell division. In only one epiphytic species, namely Rhoicosphenia curvata, were the above effects not well pronounced. The small number of species and the low standing crop of the episammic communities was possibly due to the limited number of forms that can survive frequent periods of burial. Large scale detachments were apparently correlated with a high photosynthetic rate and this was probably the reason for the many sharp falls in the number of attached algae during the summer. Algal numbers in the plankton occasionally fell in response to a loss of buoyancy of the predominant species. Although there were some exceptions, the level of nitrogen, phosphorus, silicon and carbon did not generally appear to restrict numbers. In the Avon River, however, competition with Stephanodiscus hantzschii for silicon greatly limited the standing crop of the benthic algae for short periods during the summer. For similar reasons, the epipelic, epilithic and planktonic communities remained poorly developed in areas where Cladophora glomerata occurred abundantly. In most instances, the potamoplankton was derived largely from the epipelic assemblages.

The studies on the non-parasitic brook lamprey showed that one of the major adaptations to the lengthy non-trophic periods of metamorphosis and sexual development is the accumulation of large lipid reserves at the end of the larval phase. There is also some indication that a particular lipid threshold level has to be reached before metamorphosis is initiated. The exceptionally high lipid values in the adult river lamprey at the end of the marine trophic phase are also apparently necessary to cope with the energy demands of migratory movements, spawning activity and the development of the gonads. These findings on lipid deposition and utilization are similar to those found in many other groups of animals. For example, the amount of lipid deposited in some insects is increased in the period immediately prior to metamorphosis (see Driver, Sugden and Kovach, 1974), while in the sockeye salmon, Onchorhynchus nerka (Walbaum), the lipid stores built up by the end of the marine phase of the life cycle are depleted by 91% during the subsequent spawning migration (Idler and Clemens, 1959).

The data on lipids also indicate that for accurate assessments of patterns of change, the values should ideally be based on the information gained through the use of the same techniques. The higher values recorded in this study, compared with the equivalent values expressed in terms of wet weight by Hardisty (1956) and Bull and Morris (1967), are in fact almost certainly due to the process of oven drying and the extraction with either acetone or ether. The effect of heating will for example almost certainly lead to a loss of some lipids while the use of the extraction chemicals they employed can lead to a variable extraction of the phospholipids (Love, 1970). The same reasons probably account for the slightly lower values given by Hardisty (1956) for autumn adult migrants from the River Severn. At the same time the lipid values recorded by Lanzing (1957) for animals caught in November fall between those obtained in this study for animals caught in the estuary at Oldbury and those at Tewkesbury after the animals had entered freshwater. Here again Lanzing's technique varied in that, prior to extraction with ether, he boiled the homogenate for $2\frac{1}{2}$ h in an alcoholic potassium hydroxide solution.

As was the case with algae, the marked changes in the numbers of particular crustaceans in the Severn Estuary at different times of the year means that there would be considerable variation in the availability of these as a food source for many teleost species. The decline in numbers of Gammarus in May and June was for example accompanied by a similar trend in their abundance in the gut, while the reverse pattern was observed with respect to Neomysis. In the case of the crustaceans, changes in their size throughout the year and differences in their pattern of vertical distribution also effect their relative availability. The first of these points was clearly shown in the feeding studies with sprats where Crangon only formed an important component of the diet when they were of relatively small size. In terms of vertical distribution, the presence of Eurydice near the top of the water column, where few fish feed, together with its high activity, were apparently the major reason why this comparatively common animal formed only a relatively minor component of the diet of fishes in this region.

Another factor influencing the utilization of prey by the fishes was the nature of the "escape reaction" of the crustaceans. Thus Crangon, and particularly its larger representatives, were for many species difficult to capture because of its ability to respond to the approach of potential predators with quick evasive movements. Variability in the source of food was also related to the type and efficiency of the hunting behaviour, extreme examples being provided by the less obvious approach of eels compared with that exhibited by flounders. Furthermore, seasonal differences in food source could also apparently be related to the effect of temperature. Thus, in flounders, the relatively sedentary polychaetes became of greater relative importance during the winter months. In the reservoir, another factor that was clearly of importance was the high turbidity of the water which was shown by laboratory studies to influence the size and type of prey ingested and also the distance at which fish could detect potential food. The high turbidity may also have been associated with a certain reduction in the quality of the environment in the reservoir and thus account for the slower growth rate of Crangon than was observed at Berkley and for the smaller size attained at maturity compared with the results reported by Lloyd and Yonge (1947) prior to the introduction of the Oldbury Power Station.

In summary, although many workers have empasised the "opportunistic" nature of feeding in fishes, the results of this study indicate that there are many factors which can influence the size and type of food ingested by carnivorous fishes.

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12. APPENDIX 1 Annotated list of algae collected during the investigation. Percentages refer to relative abundance by numbers. Volumes are given for the common species.

DIVISION - Bacillariophyta

Achnanthes affinis Grun. Rare, restricted to the epipelic communities of the Avon and Wylye where it represented less than 0.01% of the algae.

A. clevei Grun. Recorded only once from the Avon.

A. deflexa Reim. Recorded once from the tributary.

A. exigua Reim. Restricted primarily to the sediments of Highland Water, representing less than 0.01% of the flora.

A. exigua v. *heterovalvata* Krasske Recorded only once.

A. hungarica Grun. Recorded on two occasions.

A. lanceolata (Bréb) Grun. Widespread and common, occurring everywhere except in the episammic community. Maximum development (40%) was recorded in the epiphytic assemblages of the Wylye, its tributary and the canal. Volume = 500 μm^3

A. lanceolata f. *ventricosa* Hust. Occurring with the nominate variety, accounting for up to 10% of the epiphytic flora.

A. lanceolata v. *apiculata* Patr. Recorded on one occasion from the sediments of the Avon.

A. lanceolata v. *dubia* Grun. Occurring coincidently with the nominate variety, representing up to 6% of the epiphytic communities.

A. lanceolata v. *elliptica* Schulz. Widespread but rare, not exceeding 0.01% of the algae.

A. linearis (W. Sm.) Grun Widespread but once again rare, exhibiting maximum development (0.1%) in the epiphytic communities. Volume = 150 μm^3

A. marginulata Grun. Restricted primarily to the epipelic assemblage in Highland Water where it represented up to 4% of the flora during the spring.

A. microcephala (Kz.) Grun. Widespread but rare reaching greatest abundance (0.05%) in the epiphytic communities.

A. minutissima Kz. Occurring everywhere with maximum abundance (2%) being recorded on Cladophora in the canal. Volume = 100 μm^3

A. minutissima v. cryptocephala Grun. One of the most common taxa in the study area, frequently predominant particularly in the summer, reaching greatest abundance (up to 80%) as an epiphyte in the canal. Volume = 80 μm^3

A. saxonica Krasske Restricted entirely to Highland Water where it represented up to 99.5% of the epilithic algae and 75% of the epipelic flora. Most of the specimens, 65%, fitted illustration No. 7 of Carter (1970), with smaller numbers, i.e. 25 and 8%, being best represented by Figs 30 and 27 respectively. Volume = 300 μm^3

Amphipleura pellucida Kz. Found mainly on the sediments of Wellow Brook during the spring when it represented up to 1.0% of the flora.

Amphora coffaeiformis v. borealis (Kz.) Cl. Found on one occasion in the potamoplankton of the River Avon.

A. ovalis Kz. Collected from most habitats in all six rivers reaching greatest abundance (5%) in the epipelic communities of the Wylye, its tributary and the Avon during the winter. Volume = 2,000 μm^3

A. ovalis v. pediculus Kz. Widespread and common, often accounting for 5% of the epipelic assemblages in all six rivers particularly in the winter. Predominant on the rocks in fast flowing reaches of the Wylye as well as in the episammic community. Volume = 100 μm^3

A. veneta Kz. One specimen was observed in the epilithic community of the tributary.

Anomoeoneis sphaerophora (Kz.) Pfit. Recorded on three occasions.

Asterionella formosa Hass. Recorded only from the plankton of the Avon during the spring when it represented up to 2% of the algae. Volume = 500 μm^3

Caloneis amphisbaena (Bory) Cl. Found in the epipelic community of all six rivers as well as on the rocks in the Avon, seldom representing more than 1% of the flora. Volume = 6,000 μm^3

C. bacillum (Grun.) Cl. Most common (1%) on the sediments of Highland Water, occurring in much smaller numbers in the other rivers.

Campylodiscus noricus v. *hibernica* (Ehr.) Grun. Only two specimens were observed.

Cocconeis pediculus Ehr. Widespread but common only as an epiphyte, attaining maximum numbers (30%) on *Cladophora* in Wellow Brook where the water flowed slower than 45 cm/sec. Volume = 2,000 um^3

C. placentula (Ehr.) Cl. Occurring primarily as an epiphyte in the canal and Wylye where its abundance occasionally exceeded 10%. Volume = 1,000 μm^3

C. placentula v. *euglypta* (Ehr.) Cl. A widespread and common form reaching greatest abundance (51%) as an epiphyte on *Cladophora* in Wellow Brook where the water flowed slower than 45 cm/sec. Volume = 800 μm^3

C. placentula v. *lineata* (Ehr.) Cl. Rare, restricted primarily to the epiphyte assemblage in Wellow Brook.

C. thumensis May. Recorded only once from the potamoplankton of the tributary.

Cyclotella comta v. *genuina* A. Cl. Rare, except in the Wylye and its tributary where it represented 20% of the epipelic communities during June 1973. Volume = 400 μm^3

C. comta v. oligactus (Ehr.) Grun. This variety, plus the following two, were restricted to the sediments of the Wylye with maximum numbers (3% in v. oligactus) occurring coincidently with that of v. genuina. Volume = 400 μm^3

C. comta v. paucipunctata Grun. Greatest abundance = 1%. Volume = 400 μm^3

C. comta v. radiosa (Grun.) A. Cl. Greatest abundance = 0.1%. Volume = 400 μm^3

C. kutzingiana Thwaites Only three cells were found.

C. meneghiniana Kz. Widespread, occurring in virtually all habitats in all six rivers attaining maximum development (10 - 15%) on the sediments of the Wylye, its tributary and the Avon. Volume = 400 μm^3

C. stelligera Cl. and Grun. Widespread among the planktonic communities occurring most abundantly (3%) in the Avon early in the summer. Volume = 100 μm^3

C. stelligera v. tenuis Hust. Restricted primarily to the plankton and sediments of the Avon reaching greatest numbers (11%) in the latter habitat early in the summer. Volume = 100 μm^3

Cymbella affinis Kz. Although found in all rivers, occurring mainly in the epilithic community of the tributary with greatest numbers (12%) being observed in the autumn and spring. Volume = 1,000 μm^3

C. caespitosa (Kz.) Brun. Widespread, particularly on the sediments, but occurring most commonly (greater than 10%) on the rocks and Cladophora in the tributary during the spring. Volume = 380 um^3

C. cistula v. genuina May. Recorded on three occasions.

C. cymbiformis (Kz.) Bréb. Recorded primarily as an epiphyte from the canal representing 2.5% of the flora on Cladophora during March 1973.

C. hustedii Krasske Recorded only once.

C. microcephala Grun. Widespread but usually rare, accounting for 1 - 3% of the epilithic flora in the tributary and up to 4% as an epiphyte in the canal on occasion.

C. naviculiformis Auers. Restricted entirely to the sediments and potamoplankton of Highland Water, reaching greatest numbers (38.5%) during the spring, 1973. Volume = 1,000 μm^3

C. prostrata v. genuina (Berk.) Cl. Occasional cells were seen in the epipelic and epiphytic communities of all rivers.

C. similis Patr. Only two specimens were recorded.

C. sinuata v. laticeps A. Cl. Widespread but usually rare, found most frequently (2%) as an epiphyte in the canal.

C. sinuata v. ovata Hust. Restricted primarily to the epiphytic assemblages in the canal where its greatest abundance never exceeded 0.5%.

C. sinuata v. typica A. Cl. Recorded on three occasions.

C. tumida (Bréb.) V.H. Recorded on five occasions.

C. turgidula Grun. Recorded on eleven occasions.

C. ventricosa Ag. Widespread on the sediments and rocks normally representing lass than 2% of the flora but exceeding 10% on the rocks in the tributary during December 1973 and the following spring. Volume = 800 μm^3

C. ventricosa v. minuta (Hilse) A. Cl. Occurring primarily in the epilithic community of the tributary during December 1973 where it represented up to 6% of the algae.

C. ventricosa v. paucistriata A. Cl. Observed only seven times, mostly from the epilithic assemblage in the tributary.

C. ventricosa v. splendida A.Cl. Recorded on eight occasions from the sediments of Highland Water.

Cymatopleura elliptica (Bréb.) W. Sm. Widespread but rare, never more than twenty cells being recorded from a particular habitat throughout the investigation.

C. solea (Bréb.) W. Sm. This species(plus the following two varities) was widespread but occurred abundantly only on the sediments of the Avon during the spring where its maximum abundance never exceeded 3%. Volume = 7,000 μm^3

C. solea v. _apiculata_ (W.Sm.) Ralfs. Maximum abundance = 1.5%. Volume = 3,200 μm^3

C. solea v. _subconstricta_ f._minor_ A.Cl. Recorded on ten occasions .

Denticula tenuis Kz. Recorded on twelve occasions.

Diatoma tenue Ag. Found only on the sediments of the canal and Wellow Brook where it represented up to 0.5% of the flora. Volume = 200 μm^3

D. tenue v. _elongatum_ Lyngb. Restricted to the sediments of the canal where it represented no more than 0.01% of the flora. Volume = 300 μm^3

D. vulgare Bory Widespread, occurring in all habitats, occasionally reaching dominance, particularly in the spring as an epiphyte on _Cladophora_ in slowly moving water. Volume = 800 μm^3

D. vulgare v. _breve_ Grun. Widely distributed, occurring most frequently (11%) on the rocks and _Cladophora_ in Wellow Brook during the spring. Volume = 600 μm^3

D. vulgare v. _linearis_ V.H. Comparatively restricted, found only in Wellow Brook where its maximum abundance never exceeded 0.05%.

D. vulgare v. _producta_ Grun. This variety occurred coincidently with _D. vulgare_ but its maximum abundance but its maximum abundance never exceeded 11%. Volume = 900 μm^3

Diploneis elliptica (Kz.) Cl. Observed on seven occasions.

D. oblongella (Naeg. ex Kz.) Ross Rare, found mainly on the sediments of the Wylye and Avon, not exceeding 0.01%.

D. oculata (Bréb.) Cl. Recorded on nine occasions.

Epithemia turgida (Ehr.) Kz. Usually absent but representing 3.5% of the algae on the sediments of the tributary during February 1974.

Eunotia arcus Ehr. Restricted primarily to Highland Water, attaining greatest development (3 - 4%) in the winter and spring. Volume = 3,100 μm^3

E. curvata (Kz.) Lagerst. Normally absent but representing up to 20% of the potamoplankton in the tributary during September 1973; 3% of the epiphytes in the canal and 11% of the epilithic flora in Highland Water during the summer. Volume = 4,000 μm^3

E. exigua (Bréb.) Grun. Restricted to Highland Water, exhibiting maximum development (3%) in the spring. Volume = 500 μm^3

E. lunaris v. subarcuata (Naeg.) Grun. Found mainly in the potamo - plankton of the canal representing up to 3% of the flora during the spring. Volume = 3,700 μm^3

E. maior (W. Sm.) Rabh. Observed on two occasions.

E. pectinalis v. minor (Kz.) Rabh. Common during the autumn in the Wylye , its tributary and the canal representing from 6 to 16% of the flora, but otherwise rare or absent. Volume = 800 μm^3

E. perpusilla Grun. Recorded on eight occasions.

E. tenella (Grun.) Hust. Restricted primarily to Highland Water, reaching greatest development (3 - 5%) in the spring. Volume = 500 μm^3

E. valida Hust. Accounting for 17% of the epiphytes on Cladophora in the tributary during September 1973, and 4% of the potamoplankton of the canal in the summer 1974 but otherwise rare.

Fragilaria capucina Desm. Widespread on the sediments but rare, never exceeding 0.05%.

F. capucina v. acuta Grun. This variety occurred in all habitats but never exceeded 1% of the flora. Volume = 250 μm^3

F. capucina v. lanceolata Grun. Widespread and common, found in all habitats, with numbers often exceeding 10% in the Wylye, its tributary and the canal. Volume = 250 μm^3

F. capucina v. mesolepta Rabh. Recorded on seven occasions.

F. construens (Ehr.) Grun. Widespread, occasionally dominant in the episammic community and common (up to 12%) on the sediments of the Wylye but otherwise rare. Volume = 50 μm^3

F. construens v. binodis (Ehr.) Grun. Recorded only once.

F. construens v. venter (Ehr.) Grun. Recorded mainly from the episammic community where its abundance never exceeded 0.5%. Volume = 70 μm^3

F. intermedia Grun. Widespread and common, especially on the rocks and sediments of Wellow Brook and the Wylye where its abundance often exceeded 10%.

F. leptostauron (Ehr.) Hust. Common (10%) during the autumn of 1973 in the epipelic community of the Wylye but otherwise rare. Volume = 450 μm^3

F. leptostauron v. dubia (Grun.) Hust. Recorded on seven occasions.

F. pinnata Ehr. Rare, never exceeding 1% of the flora. Volume = 150 μm^3

F. pinnata v. intercedens (Grun.) Hust. Recorded on five occasions.

F. pinnata v. lancettula (Schum.) Hust. Recorded on five occasions.

F. virescens Ralfs Usually rare or absent, but representing 4.5% of the epipelic flora in the Wylye during March 1974.

Frustulia rhomboides (Ehr.) DeT. Restricted primarily to Highland Water, accounting for 5% of the epipelic flora in the spring. Volume = 3,500 μm^3

F. rhomboides v. saxonica (Rabh.) DeT. Restricted to Highland Water attaining maximum abundance (2%) coincidently with the nominate variety. Volume = 3,000 μm^3

F. vulgaris (Thwaites) DeT. Widespread but rare, maximum abundance not exceeding 0.1%.

Gomphonema acuminatum Ehr. Recorded on fourteen occasions, mainly as an epiphyte in the canal.

G. acuminatum v. brebissonii (Kz.) Cl. Although usually rare, this species represented 8% of the potamoplankton in the canal during October 1973.

G. acuminatum v. coronatum Ehr. Found mainly on the rocks in Highland Water, where it attained maximum numbers (13%) during the summer of both years.

G. acuminatum v. laticeps Ehr. This variety represented 5.5% of the flora on the rocks in Highland Water during the summer but otherwise remained rare.

G. angustatum (Kz.) Grun. Widespread, but found primarily on water cress and Cladophora in the canal with greatest numbers (4.5%) occurring in the winter.

G. augur Ehr. Found only as an epiphyte in the canal and the Avon, representing up to 1.5% of the flora early in the summer.

G. bohemica Reich and Fricke Recorded primarily during the colder months as an epiphyte in the canal representing up to 4.5% of the flora.

G. constrictum Ehr. Widespread, generally rare but representing 10% of the potamoplankton on the Wylye on one occasion. Volume = 1,800 μm^3

G. constrictum v. capitatum Ehr. Rare, occurring primarily as an epiphyte, not exceeding 0.05% of the flora.

G. constrictum v. subcapitatum Ehr. Found mainly on the rocks in Highland Water during the summer, maximum abundance averaging 13%. Volume = 1,300 μm^3

G. intricatum Kz. Rare, not exceeding 0.1% as an epiphyte in the canal.

G. intricatum v. _dichotomum_ May. Recorded on four occasions.

G. intricatum v. _pulvinatum_ (A.Br.) Grun. Occurring coincidently with v. _pumilum_ but not exceeding 0.5% of the flora.

G. intricatum v. _pumilum_ Grun. Restricted almost entirely to the epiphytic assemblages in the canal, occurring primarily (up to 15%) during the summer. Volume = 150 μm^3

G. montanum (Sch.) V. H. Widespread on the sediments and _Cladophora_ exhibiting maximum development (2%) in the canal during the summer.

G. olivaceum (Lyngb.) Kz. Widespread and common, frequently representing 2 - 5% of the flora on the sediments, rocks and plants in the Wylye, its tributary and the canal, with greatest numbers (up to 20%) occurring during the Winter. Volume = 500 μm^3

G. olivaceum v. _balticum_ Cl. Widespread and often common (1 - 5%) occurring in most habitats in all six rivers; representing more than 10% of the epiphytic flora in the canal, the Wylye and its tributary, particularly in the winter. Volume = 800 μm^3

G. olivaceum v. _minutissima_ Hust. A frequent (2 - 5%) epiphyte in the canal, the Wylye and its tributary which was also occasionally well represented (10%) on the rocks in the tributary during the winter. Volume = 350 μm^3

G. olivaceum v. _tenellum_ Rare, seldom representing more than 0.1% of the flora.

G. parvulum (Kz.) V.H. Widespread, found in all habitats, accounting for more than 10% of the flora on several occasions, particularly as an epiphyte. Volume = 350 μm^3

G. parvulum v. _exilissimum_ Grun. Widespread but seldom as common as the nominate variety, maximum abundance not exceeding 5% of the flora. Volume = 400 μm^3

G. parvulum v. micropus (Kz.) Cl. Recorded only once.

G. parvulum v. subellipticum Cl. Recorded on six occasions.

G. subclavatum Grun. Found mainly as an epiphyte in the canal and the River Wylye, representing up to 5% of the flora in the spring. Volume = 900 μm^3

G. tergestinium Grun. Restricted to the epiphytic assemblages in the canal, attaining maximum abundance (4%) during the winter. Volume = 150 μm^3

Gyrosigma attenuatum (Kz.) Rabh. Restricted primarily to the sediments of the River Avon where it attained a maximum abundance of 0.08%.

G. scalproides (Rabh.) Cl. Recorded on three occasions.

G. spencerii (W.Sm.) Cl. Normally rare but on one brief occasion represented up to 11% of the epilithic flora in Wellow Brook.

Hantzschia amphioxys (Ehr.) Grun. Normally rare, but representing up to 1.5% of the epipelic flora in the Avon and Wellow Brook on occasion.

H. amphioxys v. capitata O. Mull. Recorded only once.

Melosira distans (Ehr.) Kz. Found only on the sediments of Highland Water attaining greatest abundance (2%) in the spring of 1973. Volume = 200 μm^3

M. varians Ag. Found in all habitats, frequently common and sometimes achieving dominance. Volume = 1,000 μm^3

Meridion circulare (Grev.) Ag. Widespread but most common on the rocks and sediments of the Wylye and its tributary occasionally representing more than 10% of the flora, particularly in the spring. Volume = 600 μm^3

M. circulare v. capitata (Ralfs) V.H. Recorded only twice.

Navicula accomoda Hust. Recorded on four occasions.

N. bacillum Ehr. Recorded on seven occasions.

N. capitata Ehr. Widespread among epipelic communities but not exceeding 0.5% of the flora. Volume = 400 μm^3

N. cryptocephala Kz. Widespread but usually rare, maximum abundance not exceeding 0.5% except on the sediments of Highland Water and Wellow Brook where values of 8 and 5% were recorded in the spring. Volume = 1,000 μm^3

N. cryptocephala v. veneta (Kz.) Rabh. Widespread in most habitats, normally representing less than 2% of the flora but attaining considerably greater importance (10 - 15%) on the rocks in Wellow Brook and in the tributary during the autumn. Volume = 600 μm^3

N. cuspidata (Kz.) Kz. Recorded on nine occasions.

N. cuspidata v. ambigua (Ehr.) Cl. Normally absent but on one brief occasion (February 1974) represented 4.5% of the epipelic algae in the tributary. Volume = 3,400 μm^3

N. digitoradiata (Greg.) As. Recorded only twice.

N. elginensis (Greg.) Ralfs. Widespread on the sediments but never representing more than 0.5% of the flora.

N. exigua Greg. ex Grun. Rare, reaching maximum abundance (0.5%) in Highland Water.

N. gregaria Donk. Relatively common in most habitats, achieving greatest numbers (30%) during the autumn on the sediments of Wellow Brook. Volume = 450 μm^3

N. krasskei Hust. Recorded primarily from the epilithic community in Wellow Brook representing 15% of the flora during the summer, 1974. Volume = 200 μm^3

N. lanceolata (Ag.) Kz. Widespread but never representing more than 2% of the flora. Volume = 750 μm^3

N. menisculus v. upsaliensis (Grun.) Grun. Widespread, representing up to 5% of the epipelic flora in the Wylye, its tributary and the Avon. Volume = 800 μm^3

N. minima Grun. Restricted primarily to the sediments in Wellow Brook achieving notable abundance (11%) only during October 1973. Volume = 100 μm^3

N. mutica Kz. Widespread but usually rare, greatest numbers (6%) occurring during the summer in the epilithic community of Wellow Brook. Volume = 500 μm^3

N. mutica v. nivalis (Ehr.) Hust. Rare (0.1%), occurring coincidently with the nominate variety.

N. oblonga (Kz.) Kz. Rare, representing up to 0.4% of the epipelic flora in the Avon. Volume = 8,000 μm^3

N. odiosa Wallace Widespread and common on the sediments and rocks, occasionally representing up to 8% of the flora. Volume = 400 μm^3

N. pelliculosa (Bréb ex Kz.) Hilse Restricted primarily to the epilithic community of the tributary, representing 12% of the flora during February 1974. Volume = 200 μm^3

N. protracta Grun. Rare, never representing more than 0.1% of the flora.

N. pupula Kz. Widespread on the sediments, usually occurring in small numbers except in Highland Water where it accounted for 5% of the flora during March and in the tributary representing up to 8.5% of the algae during the summer. Volume = 1,000 μm^3

N. pupula v. capitata Skv. and Meyer Generally rare except on the sediments of Highland Water where it represented 13% of the flora during the spring. Volume = 1,100 μm^3

N. pupula v. rectangularis (Greg.) Grun. Recorded on six occasions.

N. pygaema Kz. Normally rare or absent but accounting for 3.5% of the epipelic flora in the tributary during January 1974.

N. radiosa Kz. Widespread but usually rare, seldom representing more than 1% of the flora. Volume = 2,000 um^3

N. radiosa v. tenella (Bréb ex Kz.) Grun. Seldom exceeding 0.1% of the flora.

N. rhyncocephala Kz. Restricted primarily to Highland Water where greatest numbers (2 - 4%) occurred early in the spring. Volume = 1,100 μm^3

N. rhyncocephala v. amphiceros (Kz.) Grun. Occurring coincidently with the nominate variety, seldom representing more than 0.5% of the flora.

N. salinarum v. intermedia (Grun.) Cl. Widespread but common only on the sediments of the Avon during the summer and autumn when it sometimes represented up to 11% of the flora. Volume = 1,100 μm^3

N. tripunctata (O.F.Müll.) Bory Widespread, frequently common, achieving greatest abundance (10 - 20%) on the sediments and rocks of Wellow Brook during the autumn . Although Hustedt (1930), Cleve-Euler (1951) and Patrick and Reimer (1966) give the minimum length of this species as 30 - 35 um, three specimens were recorded in the present study which measured 26 - 28 um . Volume = 1,500 μm^3

N. viridula (Kz.) Kz. Widespread on the sediments but seldom exceeding 0.5% of the algae. Volume = 2,500 μm^3

N. viridula v. avenacea (Bréb.) Grun. Recorded on seven occasions.

N. viridula f. minor V.H. Widespread and common particularly on the sediments and rocks of the Avon and Wellow Brook where the greatest numbers occurred in the spring. Volume = 1,100 μm^3

N. viridula v. linearis Hust. Recorded only twice.

N. viridula v. slesvicensis (Grun.) Cl. Recorded on two occasions.

N. vulpina Kz. Generally rare but representing up to 5% of the flora associated with Cladophora in the canal during March. Volume = 1,800 μm^3

Neidum affine (Ehr.) Pfitz. Recorded only once.

N. binode (Ehr.) Hust. Recorded on three occasions.

N. bisulcatum (Lager.) Cl. Recorded on seven occasions.

N. iridis (Ehr.) Cl. Recorded on eleven occasions.

Nitzschia acicularis W. Sm. Widespread and common during the spring, frequently predominant particularly on the sediments and in the potamoplankton. Volume = 400 μm^3

N. amphibia Grun. Widespread but rare not exceeding 1% of the flora. Volume = 200 μm^3

N. angustata v. acuta Grun. Recorded on three occasions.

N. angustata v. antiqua (Schm.) A. Cl. Recorded on seven occasions .

N. apiculata (Greg.) Grun. Widespread and common particularly on the sediments, occasionally representing 10 – 12% of the flora during the summer. Volume = 3,100 μm^3

N. bremhensis Hust. Widespread but rare seldom representing more than 0.5% of the flora.

N. dissipata (Htz.) Grun. Widespread and common in many areas, sometimes predominant. Volume = 350 μm^3

N. dissipata v. aculea (Htz.) V. H. Widespread, generally rare, but representing up to 7.5% of the epipelic flora in Wellow Brook and the Avon on occasion. Volume = 3,000 μm^3

N. dissipata v. media (Htz.) Grun. Widespread, occurring coincidently with N. dissipata, seldom accounting for more than 3% of the flora. Volume = 2,200 μm^3

N. filiformis (W. Sm.) Hust. Restricted to the sediments of the Avon, reaching maximum abundance, 0.5%, during the spring.

N. flexa Schm. Restricted to the sediments of the Avon and the Wylye where greatest numbers, 0.3%, occurred during the summer.

N. fonticola Grun. Widespread on the sediments, rocks and Cladophora in most rivers, attaining considerable importance (10 - 20%) during the winter in the tributary. Volume = 200 μm^3

N. frustulum (Kz.) Grun. Widespread but rare, not normally representing more than 1% of the flora. Volume = 350 μm^3

N. heufleriana Grun. Rare, seldom representing more than 0.5% of the flora. Volume = 3,500 μm^3

N. hungarica Grun. Widespread but rare, occurring primarily on the sediments of Wellow Brook and the Avon where it accounted for up to 1.5% of the flora. Volume = 3,300 μm^3

N. linearis W. Sm. Widespread, particularly on the sediments and rocks, achieving dominance during either March or April in several rivers. Volume = 3,200 μm^3

N. palea (Kz.) W. Sm. This species, plus the following two derivatives, were among the most common algae in all six areas. N. palea normally occurred in all habitats throughout the year, reaching maxima in March and April which often exceeded 20%. Volume = 400 μm^3

N. palea f. minuta Bleisch Found on the sediments throughout the year seldom representing more than 5% of the flora regardless of season. Volume = 200 μm^3

N. palea v. debilis Kz. Often common (20%) on the sediments of the Avon, the Wylye and its tributary, during the spring. Volume = 800 μm^3

N. recta Hantz. Restricted primarily to the Avon sediments, where it seldom accounted for more than 0.5% of the flora.

N. sigma (Kz.)W. Sm. Rare, seldom representing more than 0.05% of the flora.

N. sigmoidea (Ehr.) W. Sm. Found mainly on the sediments of the Avon, reaching maximum numbers, 0.3% during the spring.

N. sinuata v. tabellaria Grun. Recorded on five occasions.

N. sublinearis Hust. Restricted primarily to the sediments of the Avon reaching greatest abundance, 11%, coincidently with N. linearis during the spring. Volume = 2,000 μm^3

N. subtilis (Kz.) Grun. Found with v. paleacea but not exceeding 1.5% of the flora.

N. subtilis v. paleacea Grun. Widespread and common on sediments, representing up to 6% of the flora. Volume = 400 μm^3

N. thermalis v. minor Grun. Found primarily in the tributary where it represented 0.5% of the epilithic flora during the summer.

N. tryblionella Hantz. Rare, restricted to the sediments of the Wylye, its tributary and the Avon, not exceeding 0.1% of the flora.

N. vermicularis (Kz.) Grun. Restricted to the Avon where it seldom represented more than 0.2% of the epipelic flora. Volume = 2,500 μm^3

Opephora martyi Hérib. Widespread, often predominant in the episammic community; common on the sediments of most rivers during the spring particularly in the Wylye, its tributary and Highland Water. Volume = 750 μm^3

Pinnularia acuminata W. Sm. Observed on three occasions.

P. biceps Greg. Restricted primarily to Highland Water, occurring most abundantly (greater than 10%) early in the summer in the epipelic community. Volume = 1,300 μm^3

P. biceps f. petersenii Ross Restricted to Highland Water, occurring coincidently with the nominate variety but never as abundant. Volume = 800 μm^3

P. brebissonii (Kz.) Rabh. Restricted primarily to Highland Water, not exceeding more than 1% of the flora. On one occasion, February 1974, this species accounted for 8% of the epipelic flora in the tributary. Volume = 1,600 μm^3

P. divergentissima (Grun.) Cl. Restricted primarily to Highland Water where it never exceeded 0.3% of the flora. Volume = 550 μm^3

P. microstauron (Ehr.) Cl. Observed on ten occasions.

P. viridis (Nitz.) Ehr. Restricted primarily to Highland Water, occurring abundantly on the sediments and exceeding 10% of the flora during October 1973. Volume = 4,000 μm^3

P. viridis v. sudetica (Hilse) Hust. Restricted to Highland Water, occurring coincidently with the nominate variety but not exceeding 1% of the flora.

Rhoicosphenia curvata (Kz.) Grun. ex Rabh. Widespread, attaining dominance on Cladophora in rapidly flowing water; relatively common on the sediments of all rivers. Volume = 800 μm^3

Rhopalodia gibba O.F.Müll. Observed on four occasions.

Stauroneis anceps Ehr. Restricted primarily to Highland Water; normally rare but accounting for 11% of the epipelic flora during February and March 1973; common on the sediments of the Wylye briefly during July 1973. Volume = 1,800 μm^3

S. anceps f. gracilis Rabh. Restricted to Highland Water, occurring coincidently with S. anceps but never representing more than 2% of the flora. Volume = 2,000 μm^3

S. anceps f. linearis (Ehr.) Hust. Recorded on seven occasions.

S. obtusa Lagerst. Recorded only once.

S. phoenicenteron (Nitz.) Ehr. Restricted to the sediments of Highland Water, representing up to 2% of the flora. Volume = 22,500 μm^3

S. phoenicenteron f. gracilis (Ehr.) Hust. Observed on three occasions.

S. smithii Grun. Widespread in the epipelic communities but not normally exceeding 0.5% of the flora.

Stephanodiscus hantzschii Grun. Predominant in the plankton of the Avon during the summer and also appearing in large numbers on the sediments. Comparatively rare in the other rivers, not exceeding 3% of the flora. Volume = 100 and 400 μm^3

S. tenuis Hust. Restricted to the plankton of the Avon, representing 0.4% of the flora during the summer.

Surirella angustata Kz. Widespread on the sediments but seldom exceeding 0.5% of the flora.

S. ovalis Bréb. Observed on three occasions.

S. ovata v. angustata Kz. Occurring coincidently with v. minuta but never representing more than 3% of the algae. Volume = 1,600 μm^3

S. ovata v. minuta Bréb. Widespread and common, particularly in the spring when it frequently exceeded 10% of the flora in the Avon and Wellow Brook. Volume = 1,500 μm^3

S. tenera v. nervosa Schm. Restricted to the sediments of Highland Water where it represented 0.4% of the flora during June and July 1974. Volume = 20,000 μm^3

Synedra acus. Kz. Widespread but occurring abundantly only during April 1974 in the epilithic community of the tributary where it represented from 5 to 13% of the flora. Volume = 2,000 μm^3

S. affinis Kz. Recorded on five occasions.

S. minusculus (W. Sm.) Hust. Generally rare but representing 11.5% of the epilithic flora of the tributary during the spring. Volume = 300 μm^3

S. parasitica (W. Sm.) Hust. Frequently attached to Nitzschia sigmoidea in the Avon.

S. parasitica v. subconstricta (Grun.) Hust. Observed only once.

S. rumpens Kz. Widespread on sediments and rocks but seldom representing more than 0.8% of the flora. Volume = 400 μm^3

S. socia Wall. Observed on four occasions.

S. ulna (Nitz.) Ehr. This species, plus the following two varieties, occurred abundantly in Highland Water, sometimes exceeding 10% of the epipelic and potamoplankton communities. S. ulna was also usually common in many habitats in the Wylye and its tributary. Volume = 4,500 μm^3

S. ulna v. amphirhynchus (Ehr.) Grun. Volume = 5,800 μm^3

S. ulna v. danica (Kz.) V. H. Volume = 2,100 μm^3

S. ulna v. longissima (W. SM.) Brun. Observed only once.

S. ulna v. oxyrhynchus (Kz.) V.H. Normally rare but representing 13% of the epilithic flora of the tributary during the spring 1974. Volume = 4,200 μm^3

S. ulna v. subaequalis (Grun.) V. H. Observed on nine occasions.

Tabellaria fenestrata (Lyngb.) Kz. Restricted to Highland Water, representing 1.5% of the epipelic flora during March and April 1973. Volume = 2,000 μm^3

T. flocculosa (Roth.) Kz. Found primarily in Highland Water representing 10 - 13% of the epipelic flora during the spring 1973. Volume = 1,400 μm^3

DIVISION - Chlorophyta

Actinastrum hantzschii Lag. Found only in the plankton of the Avon during the summer 1974 when it represented 0.5 - 0.7% of the community. Volume = 250 μm^3

Ankistrodesmus falcatus (Corda) Ralfs Widespread in the plankton occurring most abundantly in the summer, frequently representing 1 - 10% of the community. Volume = 400 and 700 μm^3

Chlamydomonas spp. Unidentified planktonic forms, normally much rarer than *C. monadina* but representing 10 - 13% of the flora in Highland Water on occasion. Volume = 700 μm^3

C. monadina Stein Widespread in the plankton, often accounting for more than 10% of the community in the Avon, Wylye, its tributary and the canal. Volume = 700 μm^3

Chlorella sp. An unidentified planktonic form which was widespread but rare. Volume = 200 μm^3

C. cf. *ellipsoides* Gern. Recorded on nine occasions from the plankton of the Avon.

Cladophora glomerata (L.) Kz. Forming massive growths in all areas except Highland Water.

Closterium sp. An unidentified form recorded on three occasions.

C. acerosum (Schr.) Ehr. Restricted to the sediments of the tributary where it represented 0.1 - 0.2% of the flora during the summer.

C. ehrenbergii Menegh. Also restricted to the tributary representing 0.05 - 0.1% of the epipelic community.

C. lanceolatum v. *parvum* West and West Recorded on four occasions.

C. leibleinii Kz. Observed on three occasions.

C. lunula (O.F.Müll.) Nitz. This species, plus *C. parvulum*, were restricted primarily to the sediments of Highland Water, neither representing more than 1% of the flora. Volume = 375,000 μm^3

C. parvulum Naeg. Volume = 4,800 μm^3

Coleochaete sp. A few colonies were observed on water cress and pond weed in the canal during the summer.

Cosmarium sp. An unidentified form recorded on three occasions.

C. laeve Rabh. Restricted to the plankton of the Avon representing 0.2% of the flora during the spring 1973. Volume = 34,000 μm^3

Crucigenia tetrapedia (Kirch) West and West Rare or absent except in the plankton of Wellow Brook where it attained dominance during the autumn of 1973. Volume = 200 μm^3

Euastrum sp. An unidentified species recorded four times.

Mougeotia spp. Unidentified sterile filaments which were widespread on sediments and rocks achieving importance only in the epilithic community of Highland Water during the summer.

Oedogonium sp. Widespread on sediments but always rare.

Oocystis sp. Recorded primarily from the plankton of Wellow Brook and the Avon where it represented up to 2% of the flora during the summer. Volume = 10,800 μm^3

Pediastrum boryanum (Turp.) Menegh. Rare, found mainly in the plankton of the Avon and Wylye where its abundance never exceeded 0.05%.

P. duplex Mey. Generally rare but accounting for 2 - 5% of the plankton in the Wylye during the summer. Volume = 10,100 μm^3

Scenedesmus abundans (Kirch.) Chod. Restricted primarily to the plankton of the Avon where it never exceeded 0.2% of the flora.

S. armatus (Chod.) G.M.Smith Generally rare but, in the tributary, representing 2 - 5% of the flora during the summer. Volume = 500 μm^3

S. bijuga (Turp.) Lag. Widespread and common in the plankton, representing 1 - 3% of the flora during the summer. Volume = 550 μm^3

S. bijuga v. alterans (Rein.) Hansg. Occurring coincidently with S. bijuga but never as abundantly. Volume = 1,100 μm^3

S. dimorphus (Turp.) Kz. Widespread and common in the plankton, frequently representing 1 - 3% of the flora during the summer. Volume = 1,000 μm^3

S. incrassatulus v. mononae G.M.Smith Seldom representing more than 0.1% of the flora.

S. obliquus (Turp.) Kz. Widespread but seldom representing more than 1% of the planktonic flora. Volume = 500 μm^3

S. quadricauda (Turp.) Bréb. This species and v. parva were widespread and common in the plankton representing up to 10% of the flora on occasion. Volume = 1,200 μm^3

S. quadricauda v. longispina (Chod.) G.M.Smith This taxon and v. maximus were restricted entirely to the plankton of the Avon where their abundance never exceeded 0.2%

S. quadricauda v. maximus West and West

S. quadricauda v. parva G.M.Smith Volume = 400 μm^3

Selenastrum gracile Reinsch Widespread but common only in the plankton of the tributary where it represented 5 - 7% of the flora during the summer. Volume = 1,000 μm^3

Spirogyra sp. Unidentified sterile filaments, widespread but common only in the Avon.

Tetraedon sp. Restricted primarily to the Avon where it accounted for up to 0.1% of the plankton.

Tetrallantos lagerheimii Teil. This species, as well as the next one, were found only in the plankton of the Avon during the summer 1974, each representing about 0.5% of the population.

Tetrastrum staurogeniaeforme (Schroed.) Lemmer.

Ulothrix zonata (Weber and Mohr.) Kz. Widespread but usually rare.

DIVISION - Chrysophyta

Dinobryon sp. An unidentified form, never representing more than 0.1% of the flora.

D. sertularia Ehr. Widespread in the plankton but never accounting for more than 0.5% of the flora.

DIVISION - Cyanophyta

Aphanothece sp. An unidentified form, restricted primarily to the plankton of Highland Water where it achieved dominance during December 1973. Volume = 350 μm^3

Chamaesiphon incrustans Grun. Occurring primarily as an epiphyte on *Cladophora* in slow moving water, accounting for up to 45% of the flora on occasion. Volume = 300 μm^3

Chroococcus dispersus (Keissl.) Lemm. Rare in the plankton of the Avon.

Lyngbya spp. Unidentified, sometimes common, particularly on Cladophora. Volume = 50 μm^3

Merismopedia punctata Mey. Rare, seldom representing more than 0.1% of the epipelic flora.

M. tenuissima Lemm. This species was restricted primarily to the sediments where it represented up to 0.5% of the algae. Volume = 1,500 μm^3

Oscillatoria angustissima West and West Rare, except among growths of Cladophora in the canal where it represented more than 10% of the flora during March. Volume = 100 μm^3

O. brevis Kz. Widespread and common, representing more than 10% of the epilithic flora in the tributary, the Wylye and Wellow Brook on occasion. Also occurring frequently among filaments of Cladohpora in the canal and on the sediments in Wellow Brook. Volume = between 100 and 2,400 μm^3 depending on conditions.

O. geminata Menegh. This species was restricted to Highland Water where it represented from 8 - 12% of the epipelic flora between January and March 1974. Volume = 750 μm^3

O. limosa (Roth) Ag. Widespread, exceeding 10% of the epipelic algae in the Wylye and the Avon during the summer. Volume = 4,800 μm^3

O. splendida Grev. Observed on seven occasions.

O. tenuis Ag. Widespread on sediments but seldom representing more than 1% of the flora. Volume = 1,800 μm^3

Phormidium sp. This unidentified species was widespread in the epilithic communities representing up to 2.5% of the flora. Volume = 200 - 800 μm^3 depending on conditions.

P. foveolarum (Mont.) Gom. Common in the epilithic communities of most rivers where it often exceeded 10% of the flora. Volume = 200 - 800 μm^3

Spirulina major Kz. Recorded on five occasions.

S. nordstedtii Gom. Rare, seldom representing more than 0.1% of the flora.

DIVISION - Euglenophyta

Euglena spp. These unidentified species were widespread on the sediments and among the growths of *Cladophora*, representing up to 2% of the flora on occasion.

Phacus sp. Recorded on nine occasions from the canal.

P. orbicularis Hueb. Recorded on three occasions.

Trachelomonas sp. This unidentified species plus *T. volvocina* were widespread albeit rare in the plankton of most rivers. In the Wylye however, the unidentified form represented from 1 to 6% of the algae near the start of the summer. Volume = 3,000 μm

T. volvocina Ehr. Volume = 2,500 μm^3

T. volvocina v. *minuta* Fritsch Predominant in the plankton of the canal during May and June, frequently common elsewhere.